TOWARDS THE SUSTAINABLE USE OF AFRICAN WETLANDS

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PUBLISHED IN: Frontiers in Environmental Science

frontiers Research Topics

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ISSN 1664-8714
ISBN 978-2-88966-766-6
DOI 10.3389/978-2-88966-766-6

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TOWARDS THE SUSTAINABLE USE OF AFRICAN WETLANDS

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Citation: Simaika, J. P., Van Dam, A. A., Chakona, A., eds. (2021). Towards the Sustainable Use of African Wetlands. Lausanne: Frontiers Media SA.
doi: 10.3389/978-2-88966-766-6

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frontiers
in Environmental Science

EDITORIAL
published: 22 March 2021
doi: 10.3389/fenvs.2021.658871

Editorial: Towards the Sustainable Use of African Wetlands

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Keywords: Africa, wetland, river, freshwater, aquatic ecosystem, sustainability, ecosystem service

Editorial on the Research Topic

Towards the Sustainable Use of African Wetlands

The world's wetlands are hanging on to a thinning lifeline, with only 13% of their former extent remaining (Gardner and Finlayson, 2018). Wetlands in Africa probably conform to this picture, but data on trends in African wetland extent is limited (Davidson, 2014). Some indicators suggest increasing pressure on African wetlands since the 1990s, such as the decreasing WET Index (UN WCMC, 2017) and the threat status of wetland-dependent species in Africa (Gardner and Finlayson, 2018). Major threats include the development of hydropower dams, with some 200 new projects planned in Sub-Saharan Africa (Zarfl et al., 2015), continuing population growth and agricultural and urban development (Beuel et al., 2016; OECD-FAO, 2016). African wetlands are important for their global contribution to ecosystem services on which hundreds of millions of rural communities depend directly for their livelihoods (Dixon and Wood, 2003; Rebelo et al., 2010). Increasingly, the essential role of wetlands in climate change mitigation is recognized (Moomaw et al., 2018), and African countries have made remarkable progress with developing policies for wetland conservation and management. Fifty African nations are signatories to the Ramsar Convention on Wetlands, with 415 Ramsar sites (www.ramsar.org, Access date 22.01.2021). Nevertheless, implementing wise-use strategies remains challenging due to a lack of capacity for policy implementation (Ostrovskaya et al., 2013), and knowledge gaps with respect to wise-use. African countries are looking for a sustainable pathway between wetland development, for sustaining the livelihoods of millions of people; and wetlands conservation, to maintain ecosystem service and biodiversity values of wetlands (Wood et al., 2013). This Research Topic brings together contributions on their geomorphological classification, biological diversity, and ecological functioning, all relevant to the management of African wetlands.

One of the prerequisites of adequate wetland management policies is knowledge of the extent and status of wetlands in a country. Wetland inventories in Africa are often incomplete and monitoring is rare. Stephenson et al. suggest that barriers to effective monitoring range from data availability and quality to willingness and capacity to use monitoring data. They conclude that application of common, policy-relevant indicators, scaling up of traditional and appropriate new tools and protocols, and capacity and partnership building are the main tasks ahead.

Wetland management is often hindered by a lack of dedicated expertize, and declining funds. In a new cost-saving approach, Job et al. did a first full wetland inventory of Mountain Zebra National Park (South Africa) using existing data, imagery, and a participatory approach to select a subset of target sites to assess wetland condition. Significantly, none of the target sites were National Freshwater Ecosystem Priority Areas, highlighting the importance of the participatory approach. Wetland classification in South Africa emphasizes the landscape setting of wetlands as a basis for classification. Grenfell et al. propose to include the geomorphic processes of wetland formation in a new genetic geomorphic

Edited and reviewed by:
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Specialty section:
This article was submitted to
Freshwater Science,
a section of the journal
Frontiers in Environmental Science

Received: *26 January 2021*
Accepted: *09 February 2021*
Published: *22 March 2021*

Citation:
Simaika JP, Chakona A and van Dam AA (2021) Editorial: Towards the Sustainable Use of African Wetlands.
Front. Environ. Sci. 9:658871.
doi: 10.3389/fenvs.2021.658871

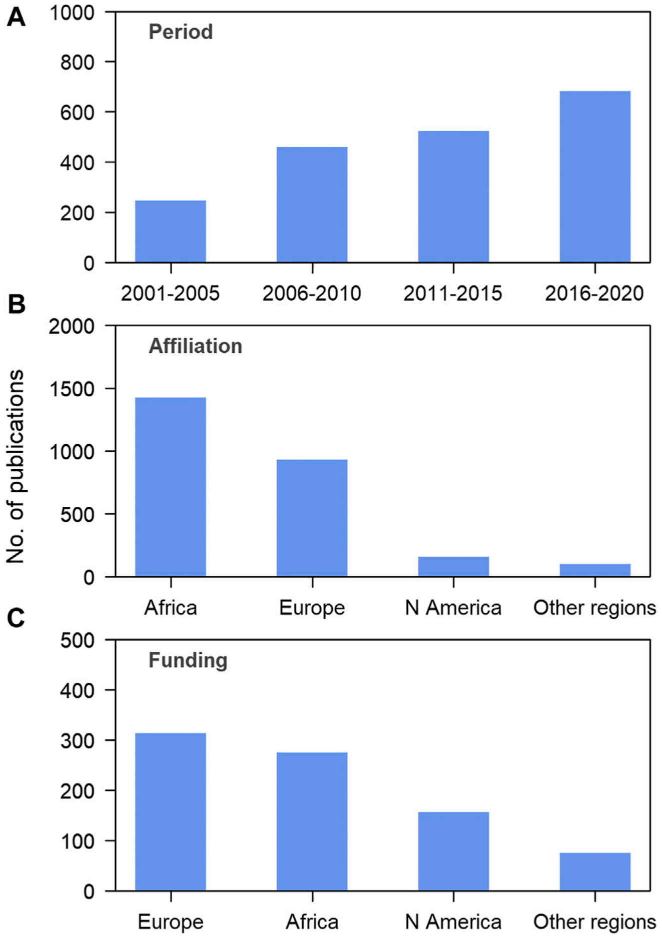

FIGURE 1 | Bar charts of Scopus (www.scopus.com) search results for 'Africa' and 'wetland' in title, abstract and keywords of published articles from 1999 to 2020 (Search date: 12.01.2021). **(A)** Publications on African wetlands over four 5-year periods (2001–2005; 2006–2010; 2011–2015; 2016–2020); **(B)** Affiliations associated with research on African wetlands categorized by world region; **(C)** Funding for research on African wetlands categorized by region.

classification system. Accordingly, the first level of the hierarchical classification considers the sediment source responsible for wetland formation, followed by the wetland type. This approach could be extended to include all wetlands and be used complementary to existing classifications. Mapping and accurately predicting wetland occurrence and extent, hydrogeomorphic (HGM) type, and ecological condition from remote sensing data remains challenging. In a case study of wetlands in the Western Cape (South Africa), Rivers-Moore et al. used a Bayesian model approach to predict hydrogeomorphic types. Four variables, groundwater depth, relief ratio, slope, and elevation were particularly important in building accurate models.

The linear nature of rivers makes the protection of many species difficult, as multiple stressors are added along the river continuum. In an analysis for the Cape Fold Ecoregion (South Africa), Jordaan el al. evaluated the protection of freshwater fishes under the existing protected area network. The results are sobering: the majority of freshwater fish species are inadequately protected. Increasingly, non-invasive sampling methods are gaining importance for monitoring freshwater fish. Castañeda et al. explored three methods for their strengths and weaknesses in the Eastern Cape (South Africa). The detection probability using visual observation methods, snorkel surveys and underwater camera trapping, were compared to environmental DNA (eDNA) sampling. In this study, the traditional visual survey methods were more efficient at detecting target species than the novel sampling method. Tropical, large shallow lakes are highly productive ecosystems. In order to manage these types of lakes both for species conservation and for inland fisheries, it is important to understand how the lake food webs respond to seasonal flooding and drying. For Lake Liambezi in Namibia, Peel et al. identified three major pelagic food chains, two benthic based, and one phytoplankton-based. The latter was the longest food-chain, involving four trophic transfers. Restoring this food chain would lend stability to the ecosystem, in which the tilapiine fishery collapsed in 2016.

Namaalwa et al. investigated the impact of surface water nutrient pollution from agriculture and urbanization on water quality and nutrient and sediment retention in the downstream

Namatala Wetland (Uganda). Nutrient concentrations were significantly higher in the urbanized streams upstream of the wetland than in the rural streams draining agriculture. The wetland did retain nutrients and sediment in the downstream part, which had more intact papyrus and lateral connectivity. Sileshi et al. investigated the potential of three natural riverine wetlands to retain pollutants and to improve water quality downstream in Jimma Town (Ethiopia). The wetlands did indeed retain pollutants, but this negatively affected the ecological integrity of the wetlands themselves. This finding highlights that water quality needs to be managed to the point that the receiving wetlands are not damaged and can effectively mitigate pollution. A second study on wetland sediment and nutrient retention also in Jimma Town by Mereta et al., supports the findings by Sileshi et al.

The idea that wetlands are converted for agriculture or human settlement mainly because they are perceived as wastelands is brought into question by the fact that despite increased awareness of the importance and value of wetlands, the habitats are continually degraded and lost. In their work on Anyiko wetland (Kenya), Ondiek et al. found that the conversion of the wetland was dependent on the socio-economic standing of households and not perception of value. Ondiek et al. suggest that a shift in the institutional regulatory framework is needed towards intersectoral collaboration and incentivization for wetland restoration. Also at Anyiko wetland, Owino et al. assessed greenhouse gas emissions from rice paddies with and without fertilizer application. Fertilization had no effect on methane or carbon dioxide emissions, but caused substantial increase in nitrous oxide emissions. Overall the study suggests that cultivation and land preparation is responsible for a loss of organic carbon, limiting the ability of the wetland to store carbon.

The water resource potential of the ephemeral Mara river system (Kenya) was explored by Wekesa et al. Although subject to losses through evapotranspiration and seepage, ephemeral rivers store significant amounts of water in the river alluvium beneath the channel bed. The authors conclude that the annual storage volume could be used as an alternative water source for communities. Whilst this could indeed be done, the current water need for livestock in the catchment already exceeds the available water storage, and would mean that no water would remain for natural fauna or flora.

The submissions to this inter- and multidisciplinary Research Topic present a wide range of research topics on African wetlands, all highly relevant to policy and management for sustainable management, such as traditional and novel monitoring methods, climate change mitigation, and water quality and quantity regulation. The number of scientific publications on African wetlands has risen in the last 2 decades, with a strong involvement of European researchers and funding (**Figure 1**). Data on wetland loss in tropical Africa is scarce (Davidson, 2014), but it seems reasonable to assume that the degree of forest and river degradation is still lower than in other parts of the world (Döll et al., 2009; Hill et al., 2019). We think that Africa can still aim for a development trajectory towards sustainable catchment management and wise use of wetlands straight away without first losing wetland ecosystem services and then having to restore them in the future, as in Europe and North America (Szałkiewicz et al., 2018). To achieve this, a major effort should go, besides the traditional conservation of protected wetlands, into strengthening integrated landscape management and sustainable agriculture and urbanization (UNCCD, 2017). With respect to research, topics not presented in this Research Topic will need more attention: adaptive governance and the roles of formal and informal institutions (McCartney et al., 2011), participation of local communities in protecting wetlands (Wood et al., 2013), ecosystem services trade-offs at the landscape level (Carpenter et al., 2009; Wangai et al., 2016; Langan et al., 2018), incentivizing conservation (Seidl et al., 2020), conservation psychology (Clayton and Brooks 2005), and economic instruments to support conservation and wise use (ten Brink and Russi, 2018).

DEDICATION

This Research Topic is dedicated to two of our colleagues who contributed enormously to the conservation of African wetlands: the late Prof. Olaf Weyl, Chief Scientist at the South African Institute for Aquatic Biodiversity and DST/NRF research Chair in Inland Fisheries and Freshwater Ecology; and the late Mr. Paul Mafabi of the Wetlands Inspection Division, later Director of Environment at the Ministry of Water and Environment, Uganda and Chair of the Standing Committee of the Ramsar Convention in 2006–2008.

AUTHOR CONTRIBUTIONS

JS and AvD drafted the manuscript. All authors reviewed and contributed to the final version of the manuscript.

ACKNOWLEDGMENTS

We would like to thank the reviewers who volunteered their time and effort in contributing to this Research Topic.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

METHODS
published: 05 November 2019
doi: 10.3389/fenvs.2019.00174

A Genetic Geomorphic Classification System for Southern African Palustrine Wetlands: Global Implications for the Management of Wetlands in Drylands

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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *08 May 2019*
Accepted: *16 October 2019*
Published: *05 November 2019*

Citation:
Grenfell S, Grenfell M, Ellery W, Job N and Walters D (2019) A Genetic Geomorphic Classification System for Southern African Palustrine Wetlands: Global Implications for the Management of Wetlands in Drylands. Front. Environ. Sci. 7:174. doi: 10.3389/fenvs.2019.00174

Due to climatic constraints in dryland regions, wetlands usually occur at confluences of flow paths, whether from surface flow, inter-flow or at locations of groundwater discharge. Long-term landscape processes that shape valleys and focus the movement of water and sediment are accountable for providing a suitable template with which hydrology interacts to allow wetland formation. Current hydrogeomorphic classification systems do not address system-scale linkages of sediment and water transport across the landscape, and are therefore unable to contextualise long-term process dynamics. Misunderstanding long-term earth system processes can result in the application of inappropriate restoration strategies that isolate wetlands from longitudinal drivers of their formation. We propose a genetic classification system that focuses on the mode of wetland formation, and is based on the understanding that genetic processes impact on the outcome hydrology, sedimentology, geomorphology, ecosystem service provision, and long-term dynamics of wetlands in drylands. The classification aims to impart understanding of dynamic processes of sediment transport through wetlands, such that restoration plans can be sensitive to long-term landscape processes. The classification system, derived from a combination of international literature and published South African case studies, has four wetland macrotypes based on sediment source (colluvial, alluvial, Aeolian, and geochemical). These are subdivided into eight wetland types; hillslope seep, floodplain, valley-bottom, plain, blocked-valley, alluvial fan, aeolian depression, and geochemical depression. The classification is based on landscape location, shape, and the occurrence of geomorphic characteristics indicative of process.

Keywords: wetland geomorphology, wetland classification, wetland restoration, wetland management, drylands

INTRODUCTION

Another Wetland Classification System?

The majority of wetlands in southern Africa are located along drainage lines due to widespread semi-arid conditions associated with the sub-tropical high pressure belt (Ellery et al., 2009). This is in contrast to more humid environments, where wetlands may occur in a wider variety of landscape settings due to a favourable water balance in which rainfall equals or exceeds evaporation. In southern Africa, with the exception of a few coastal and mountainous catchments, annual potential evaporation generally exceeds annual rainfall, in many areas by a factor of two to three (Schulze, 1997). As a result, wetlands usually occur in areas of flow accumulation concentration, whether from surface flow (channel or surface runoff) or inter-flow (within soil and bedrock), or occasionally at locations of groundwater discharge. In dryland regions (MAP:PET < 0.65; UNEP, 1997), long-term geomorphological processes and fluxes of earth surface materials shape valleys and concentrate surface and near-surface flow accumulation, providing the conditions necessary for wetland formation (Tooth and McCarthy, 2007; Tooth et al., 2015; Lidzhegu, 2019; Lisenby et al., 2019).

In this context, wetlands can be considered geomorphic systems that are dynamic in form as well as in their fluxes of water and all constituent matter (sediment, solutes), and are responsive to natural and anthropogenically-induced changes in water, sediment, and solute supply (Tooth, 2018; Lisenby et al., 2019). Wetland dynamics may respond to a combination of autogenic and allogenic forcing (Tooth et al., 2007; Larkin et al., 2017). For instance, valley-bottom wetlands become vulnerable to incision once a threshold slope (*sensu* Schumm, 1979) is exceeded for a particular catchment size and rainfall (Ellery et al., 2009, 2016). This concept was extended by Tooth (2018) for meandering river floodplain wetlands, through consideration of a threshold of wetland dynamics determined by interactions between discharge, slope, and sediment availability (supply), where systems subject to sudden and substantial morphological changes may be separated from systems subject to gradual and relatively continuous adjustments of form. In some cases, changes to catchment run-off that alter the water to sediment supply ratio may lead to either erosion (where $Q > Qs$) or aggradation (where $Qs > Q$) (Gell et al., 2009; Tooth, 2018). In other cases, changes in rates of lateral erosion and accretion reflect a change in the elevation of a geologically controlled local base level (e.g., Tooth et al., 2004; Ellery et al., 2012; Keen-Zebert et al., 2013). Changes in catchment run-off and thus rates of sediment transport, erosion or deposition may also occur naturally due to climatic oscillations (e.g., Aalto et al., 2003; Macklin and Lewin, 2003; Grenfell and Ellery, 2009) or may be forced by anthropogenically-induced climate change. Understanding the temporal and spatial scales of these dynamics, as well as the drivers behind them, is key to successful wetland management and restoration.

In this paper, we propose a new genetic geomorphic classification system that acknowledges the role of geomorphology in wetland formation (Tooth et al., 2015), and aims to connect observable geomorphic features in the landscape with the processes that created them (Buffington and Montgomery, 2013; Lisenby et al., 2019). Wetland classification systems are usually based on a selected wetland definition, the most commonly used being that of Cowardin et al. (1979), which requires that a wetland meets one or more of the following criteria: (1) it supports hydrophytes at least periodically, (2) the substrate is composed of undrained hydric soil and/or (3), the substrate is non-soil and is saturated or covered by shallow water at some time during the growing season of each year. This particular definition has been used as the starting point for several wetland hydrogeomorphic classification systems, including those of Cowardin and Golet (1995), Brinson (1993) and Semeniuk and Semeniuk (1995). According to Finlayson and van der Valk (1995), the primary reason for developing a classification system is to support wetland inventory by standardising and defining terms to describe wetland types to allow successful wetland conservation and management. We argue that a wetland classification system can be more than a system for inventory, and that it can also be used as a tool to improve understanding of wetland processes and dynamics (Kondolf and Piégay, 2016).

A failure to appropriately conceptualise natural and human induced trajectories of change in wetlands, in tandem with a lack of appreciation of the importance of longitudinal (dis)connectivity, can result in poor outcomes for wetland restoration in dryland environments. For example, the hydrogeomorphic classification scheme currently in use in South Africa, developed by Ewart-Smith et al. (2006) and Ollis et al. (2015), incorporates very little geomorphological insight beyond consideration of the landscape setting, and emphasises "product" (landscape setting) over "process" (dynamic feedbacks between process and form) geomorphology (Lisenby et al., 2019). The result is that short-term hydrological processes are considered the master variable in wetlands with developmental histories that in many cases extend over several millennia, and have been shaped by a highly complex interplay between a geological template and dynamic flows and fluxes of earth surface material (Tooth and McCarthy, 2007; Lisenby et al., 2019). As Simenstad et al. (2006) suggest, without recognising landscape dynamics, wetland restoration efforts are unlikely to realise the full ecosystem performance that is sought.

The paper sets out the physical basis of the proposed genetic geomorphic classification system by outlining a generic set of geomorphic modes of wetland formation common in dryland environments, by providing a context for geomorphic change and processes typically associated with each mode of formation, and by clarifying when and how longitudinal (dis)connectivity in material fluxes most significantly influences wetland ecological integrity. The system is considered a genetic classification as it is based on the fundamental landscape processes that result in the formation of each wetland type. The system does not consider hydroperiod explicitly, but rather aims to describe landscape setting and landform, and consider hydrologically-linked processes of sediment erosion, transport and deposition that may be associated with each wetland.

Existing Wetland Classification Systems

Cowardin and Golet (1995) developed one of the most comprehensive and widely used ecologically-based wetland classification systems for the United States. This hierarchical system can be used alongside several hydrological, soil and chemistry modifiers. This is the basis of several regional classification systems used in North America (e.g., US Federal Geographic Data Committee, 2013; Alberta Environment Sustainable Resource Development, 2015). Palustrine wetlands may be divided into seven classes based on the areal extent of either the dominant life form or substrate composition. The selection of life form and substrate as classification criteria was based on the reasoning that these would be easily identifiable, even on satellite imagery, and that they do not change seasonally. The classification is descriptive and its simplicity is useful for inventory purposes. However, a single wetland system may fall within several classes depending on the mapping resolution. Furthermore, the classification provides no indication of the processes that have resulted in the pattern of vegetation being mapped. For instance, a reed-dominated emergent wetland could occur in multiple landscape environments, such as in a tidal lagoon, on the bed of a non-perennial river or on the margins of a floodplain. Thus, while this approach is useful for cataloguing purposes, there is no indication of the geomorphic or hydrological processes that are likely to drive long-term functioning.

The Ramsar "Classification System for Wetland Type" approved by the 1990 Conference of the Contracting Parties (Recommendation 4.7) with subsequent amendments, is a broad framework for rapid identification that consists of three categories with 42 wetland types. The classification is designed for rapid assessment and is therefore not scientifically exhaustive, and makes use of a variety of inconsistently applied discriminant criteria such as geomorphic form, hydroperiod, water quality, substrate type, and vegetation type. As a result, it is possible for a single wetland to fall into multiple types. Once again, the classification is descriptive and is focussed on classifying the outcome variables (i.e., vegetation) rather than the driving factors behind wetland formation.

In contrast to these, Brinson (1993) and Semeniuk and Semeniuk (1995) focussed on landform and hydrology in order to provide a better assessment of the physical, chemical, and biological functioning of different wetland types. The underlying rationale for such an approach was that hydrogeomorphic processes could be used to classify wetlands distributed across a wide range of climatic, geological, soil, and vegetation settings.

In Semeniuk and Semeniuk (1995) geomorphic classification system for Australian inland wetlands, discrimination is based on landform and hydroperiod as these are considered the primary controls on wetland formation. For instance, in a dryland environment, a flat could be permanently dry, while in a more humid environment, the flat might be a wetland. As in Cowardin and Golet (1995), other factors such as water quality and vegetation type may be used to augment the classification. While useful for the purpose of inventory, the classification system provides no information about wetland morphodynamics, which is essential for determining a sustainable approach to wetland restoration (Ellery et al., 2009). For example, a floodplain is classified as a "seasonally inundated flat," and according to the definition, this wetland type can refer to a flat that may or may not be linked to a river. Thus, all floodplains are classed as one type, despite variations in sediment flux and exchange flux processes, and the implications of such processes for ecosystem dynamics and the delivery of ecosystem services (Kotze et al., 2009). In dryland environments, a deeper understanding of floodplain wetlands, especially with regards to flow variability and its impact on geomorphic processes, is vital if we are to fully appreciate their potential to recover following disturbance, as well as to evaluate ecosystem service delivery (Thoms, 2006; Grenfell S. E. et al., 2009).

Nanson and Croke (1992) provide a comprehensive process-based floodplain classification that is based on the ability of a river to entrain and transport sediment in conjunction with the erosional resistance of floodplain alluvium. The system has three classes (high-energy non-cohesive, medium-energy non-cohesive, and low-energy cohesive) that are sub-divided by predominant floodplain forming processes. The resultant floodplain types are distinctive in terms of morphology and genesis. Furthermore, as the classification is based on processes, it acknowledges that it is possible for floodplains to transform from one type to another. A number of similar approaches have been applied in the empirical discrimination of channel planform pattern (for relatively recent examples see Nanson and Knighton, 1996; Kleinhans, 2010; Kleinhans and Van den Berg, 2011). Although focussed on channel planform, these classifications incorporate morphodynamic processes since channel planform is dependent on feedbacks between bars, channels, floodplain, and vegetation (Kleinhans and Van den Berg, 2011).

A classification system for all inland aquatic ecosystems, including rivers and wetlands, was developed for South Africa by Ewart-Smith et al. (2006) and Ollis et al. (2015). The wetland classification builds on earlier work by Kotze et al. (1994, 2009), with the latter works largely based on Brinson (1993). The system is also hierarchical, with landscape setting incorporated at level 3 (valley floor, bench, plain, or slope). Hydrogeomorphic units, introduced at level 4, are defined according to landform, hydrological characteristics and hydrodynamics, and include river, floodplain, channelled valley-bottom, unchannelled valley-bottom, depression, seep, and wetland flat. Ollis et al. (2015) argue that the "functional unit," which may be derived at level 5 by applying a secondary discriminator (saturation period) to the hydrogeomorphic type, defines the functioning of the aquatic ecosystem. Functional units at this scale are not useful when planning restoration as this approach does not recognise that wetlands are part of an integrated drainage system with fluxes of sediment and water between functional units that are as important as the units themselves (c.f. Chorley and Kennedy, 1971). Furthermore, these fluxes shape unit dynamics over decadal to centennial timescales (e.g., Tooth et al., 2014).

In practise, many wetlands do not fit comfortably into this classification. For instance, wetlands located in blocked valleys have characteristics of valley-bottom wetlands as well as depressions (Grenfell et al., 2008, 2010). In addition, many valley-bottom wetlands are discontinuous and have reaches that are channelled and unchannelled (Grenfell M. C. et al., 2009; Grenfell et al., 2012; Tooth et al., 2014). It is also difficult to objectively determine the difference between a floodplain wetland and a channelled valley-bottom wetland, for which Ollis et al. (2015) recommend the identification of meandering river floodplain geomorphic features (e.g., backwater depressions, meander cut-offs, alluvial ridges, scroll bars, and leveés). The occurrence of these features is skewed toward identifying single-thread meandering river floodplains. From a geomorphic origin and process point of view, it is clear that the channelled valley-bottom is a type of floodplain, and there is a need to discriminate additional floodplain types characterised by floodplain features and processes (Nanson and Croke, 1992; Lisenby et al., 2019).

The decision as to what classification level or unit should be used for different levels of analysis or inventory is complicated by the inter-disciplinary nature of wetland research. Sieben et al. (2011) argue that hydrogeomorphic units exhibit similar hydrological and geomorphological characteristics, and that these units should be used in wetland restoration planning. This is consistent in principle with the view of Ollis et al. (2015). Since some ecosystem services are linked to specific habitat types, Sieben et al. (2018) suggest that in order to more accurately assess ecosystem service provision in individual wetlands, functional HGM units should be further sub-divided by vegetation class. The authors suggest that this is particularly important when considering ecosystem services that are primarily associated with the functional unit but where their delivery is modified by vegetation type. However, the division of wetland systems into smaller management units is risky as it encourages piecemeal planning and conservation efforts. For instance, if management begins to focus on conserving a specific vegetation type within a specific functional unit nested within a larger hydrogeomophic unit, the chance of success is limited by failure to recognise process-linkages between system components (Dollar et al., 2007). Flows of sediment and water occur between functional units and vegetation classes. While wetland restoration planning should consider the restoration of habitat patches in order to conserve threatened species or plant communities, this should be done at a system scale to ensure system integrity.

A GENETIC GEOMORPHIC CLASSIFICATION SYSTEM FOR PALUSTRINE WETLANDS IN DRYLANDS

Several authors have highlighted the necessity of ensuring any proposed classification and inventory system meets the needs of managing agencies and is accessible and relevant (Finlayson and van der Valk, 1995; Scott and Jones, 1995). We propose that a genetic geomorphic classification system in the context of dryland wetlands can provide more than a series of classes on which to base conservation efforts, but that this classification system will improve understanding of wetland geomorphic processes that govern the movement of water and all constituent matter through the ecosystem at varied spatial and temporal scales (Lisenby et al., 2019). Our proposed classification system considers a wetland unit to be one which meets the Cowardin et al. (1979) definition, and by integrating process and response, is associated with a particular mode of formation. The wetland unit may comprise areas that are hydrologically varied (i.e., some parts may be permanently wet, others seasonally or temporarily), but these zones are often fairly predictable based on the type or sub-type.

The first level of the hierarchical classification divides wetlands according to the dominant sediment source responsible for the formation of the wetland (**Table 1**). The wetland *macrotype* may be described as either colluvial (sediment deposited under the influence of gravity by slope processes), alluvial (sediment deposited by fluvial processes), aeolian (related to or arising from wind action), or geochemical (sediment derived from *in situ* weathering of mineral parent material and/or solution translocation and precipitation). The wetland macrotype therefore distinguishes the dominant geomorphic processes driving wetland formation.

Level 2 of the classification system describes wetland *type*, where discrimination is based on three variables; (1) landscape position (hillslope, valley or plain), (2) 3-dimensional shape (a description of cross-section and longitudinal slope), and (3) typical geomorphic features (presence or absence of channel, connectivity to channel network, and/or being within a depression). This is not an attempt to classify the wetland based on topography, but rather an acknowledgment that the landscape, particularly the wetland landform, is a product of geomorphic processes. Therefore, in contrast with Lisenby et al. (2019), we do use the terms "slope" and "flat" where required, but explicitly conceptualise these terms in the context of geomorphic mode of origin. The wetland type may be classified as a hillslope seep, hillslope plateau, alluvial floodplain, alluvial valley-bottom, alluvial plain, alluvial blocked-valley, alluvial fan, aeolian depression or geochemical depression.

Colluvial hillslope seeps, alluvial floodplains and valley-bottoms, and geochemical depressions may be further subdivided into sub-types at level 3 on the basis of process dynamics (characteristic processes of erosion and deposition, or dissolution and precipitation in the case of geochemical depressions). Hillslope seeps may be divided based on the presence or absence of discontinuous channel outflow (as in Kotze et al., 2009), valley-bottoms may be divided based on the presence or absence of a discontinuous river channel, floodplains may be discriminated based on indicators of lateral channel activity and sinuosity, while geochemical depressions may be separated based on the type of underlying bedrock. A detailed descriptor for each type and sub-type is provided below, while satellite images of distinct types are provided in **Figure 1**.

COLLUVIAL WETLANDS

Hillslope Seep Wetlands

Sediment in colluvial wetlands accumulates via colluviation from upslope as well as by *in situ* pedogenesis which is enhanced by the presence of water. Seep wetlands originate under the combined influence of topography and underlying stratigraphy, and as a

TABLE 1 | Macrotypes and types of a genetic geomorphic classification of inland wetlands for dryland regions, sub-types are provided on subsequent tables where applicable.

Level	**Discriminant**								
Macrotype	**Sediment/substrate source**	**Colluvial**	**Alluvial**					**Aeolian**	**Geochemical**
Wetland type	**Landscape position, shape and geomorphic features**	**Hillslope seep**	**Floodplain**	**Alluvial valley-bottom**	**Alluvial blocked-valley**	**Alluvial plain**	**Alluvial fan**	**Aeolian depression**	**Geochemical depression**
Description	Landscape position	Hillslope	Valley	Valley	Valley	Plain	Hillslope, valley, or plain	Plain or valley	Plain or valley
	3D Shape	In long profile, thalweg elevation decreases with distance downstream. Occasionally on a colluvial drainage line, but not always.	Has a discernible valley boundary. In long profile, thalweg elevation decreases with distance downstream. Longitudinal slope of a floodplain is typically lower than that of a valley-bottom wetland. In cross-section, valley is fairly flat, although there may be micro topography associated with river specific processes.	Has a discernible valley boundary. In long profile, thalweg elevation decreases with distance downstream. Longitudinal slope of a valley-bottom is typically steeper than that of a floodplain. In cross-section, valley is fairly flat, although there may be micro topography associated with floodouts in the case of discontinuous valley-bottom wetlands.	Similar to a floodplain or valley-bottom in cross-section, but on long profile it is broadly concave, similar to a depression.	No obvious valley boundary, planar feature, extremely flat and broad.	Convex shaped sediment deposit on a flat valley floor	Concave depression	Concave depression
	Geomorphic features	It may or may not have an outflowing stream.	Characterised by a channel or channel network located within a valley.	A valley surface that is characterised by either no channel or a series of discontinuous channel reaches	Located on a drainage line that has been blocked by deposition on either the main stem or tributary channel. There may be a lake or a tie channel linking the blocked valley to the drainage network downstream.	Occurs on a large flat plain with no discernible slope. Disconnected from drainage networks.	Characterised by a distributary network branching from an upstream node. May be located on hillslopes, floodplains or alluvial plains.	A depression that has been created in unconsolidated aeolian sediments by wind erosion.	A depression that has been created by geochemical weathering (typically through hydroloysis on igneous rocks, carbonation on limestone rocks or repeated redox reactions on Fe rich rocks). It may or may not have an inflowing and/or outflowing stream.

Map data: Google, CNES / Airbus, DigitalGlobe, Landsat / Copernicus, TerraMetrics

FIGURE 1 | Google Earth images of representative wetland types and sub-types, scale is variable to ensure visibility of features. **(a)** Hillslope seeps with and without stream, Swartberg, South Africa; **(b)** discontinuous valley-bottom, Mooi River catchment, South Africa; **(c)** unchannelled valley-bottom, Ntsikeni, South Africa; **(d)** blocked-valley depression, Muzi pan with Mkuze River towards south, South Africa; **(e)** straight river floodplain, Lotheni River, South Africa; **(f)** sinuous river floodplain, Okavango Delta, Botswana; **(g)** meandering river floodplain, Mzimvubu River, South Africa; **(h)** anastomosed river floodplain Okavango Delta, Botswana; **(i)** mixed bedrock-alluvial anabranching river floodplain, Orange River, South Africa; **(j)** wandering river floodplain, Olifants River, South Africa; **(k)** alluvial flat, Agulhas Plain, South Africa; **(l)** alluvial fan, Linyanti Swamp, Botswana; **(m)** aeolian depression, Verneukpan, South Africa; **(n)** subsidence depression, Dartmoor, South Africa; **(o)** redox depression, Shadowvlei, South Africa; **(p)** dissolution depressions, Ubib embayment, Namibia; and **(q)** margin-aggradation depression, Okavango Delta, Botswana.

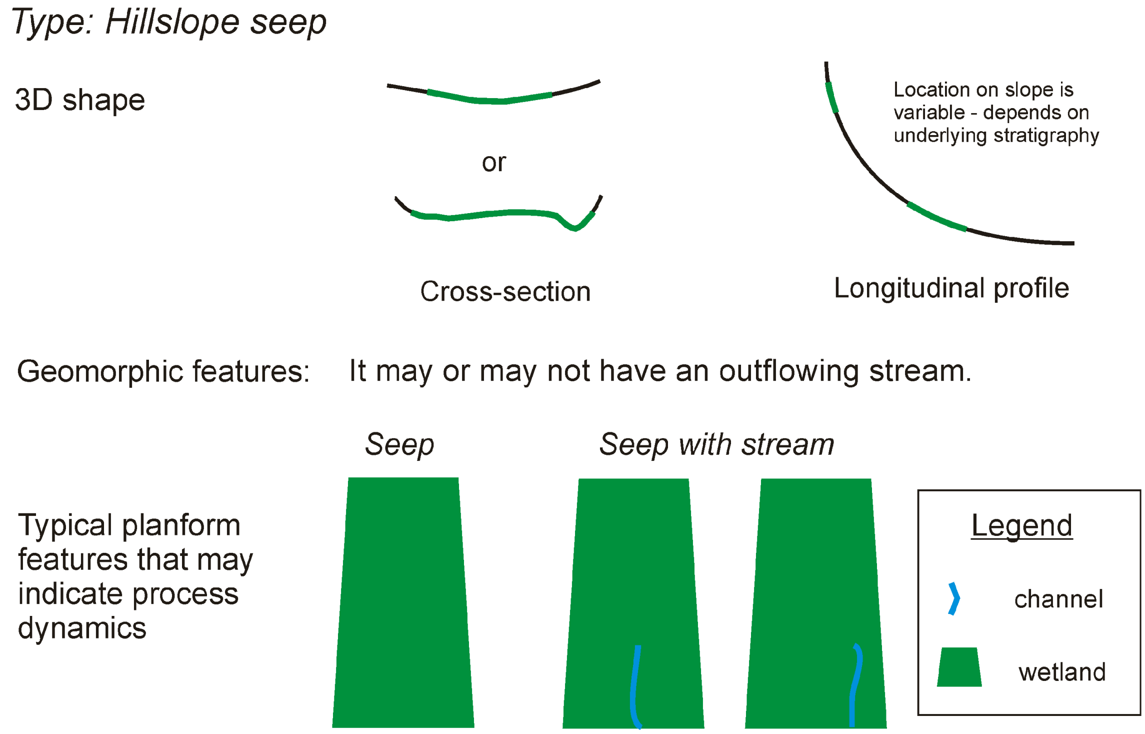


FIGURE 2 | Schematic shape and geomorphic features that are used to classify hillslope seep wetland type, followed by typical planform features that are process indicators used to classify wetland sub-type.

TABLE 2 | Description of hillslope seep sub-types.

Macrotype	**Sediment source**	**Colluvial**	
Type	**Landscape position, shape and geomorphic features**	**Hillslope seep**	
Sub-type	**Process dynamics (characteristic processes of erosion and deposition)**	**Seep**	**Seep with stream**
Description	**Hillslope seeps:** Presence or absence of stream	No stream	Base of hillslope wetland flows into a small stream

result, Brinson (1993) discriminates between topographic seeps, which form at the convergence of lateral subsurface water in concave areas, and stratigraphic seeps which occur where a slope intersects the lateral flow of water. In dryland environments, hillslope topographic seeps fed by regional groundwater aquifer discharge have a restricted distribution associated with relatively rare artesian flow systems. Instead, almost all hillslope seeps are stratigraphic and form where a layer with restricted permeability deflects water that has filtered through the soils of the upper slope via gravity. The layer of restricted permeability may occur either at the soil/bedrock interface or within the soil where there is a change in soil texture associated with reduced hydraulic conductivity (Kuenene et al., 2011, 2013; Van Tol et al., 2011). The relative source area of water contribution determines the degree of saturation as well as the duration and timing of inundation of the seep wetland (Jaeger et al., 2007; Job and Le Roux, 2018).

The landscape form of seep wetlands is variable (**Figure 2**). Hillslope longitudinal slope can range from very steep to relatively flat, provided there is sufficient slope for unidirectional subsurface flow of water. Cross-sectional morphology can range from slight to moderately concave. Such wetlands have a low hydraulic radius and high roughness due to dense vegetation cover, which both contribute to diffuse flow. All hillslope seep wetlands are vulnerable to activities in the catchment that interrupt or reduce the infiltration and percolation of water into the sub-surface soil and/or rock, such as the introduction of hardened surfaces or development of tree plantations. Hillslope seep wetlands may be divided into sub-types on the basis of the geomorphic process of channel initiation which has implications for processes of sediment transport downslope (**Table 2**).

Seep

In situations where subsurface discontinuities in geological units (e.g., faults) or water-bearing geologies (e.g., fractured bedrock) intersect the ground surface, the water source may be expressed as localised patches that are seasonally to permanently wet within the overall seep wetland. Depending on the size and climate of the source area, flows may maintain saturated conditions year-round, resulting in a shallow but predictably stable local water-table. Continuous water replacement may result in more frequent oxidising conditions relative to the more dominant reducing conditions of stagnant saturated soils.

Seep With Stream

Streams are initiated when a threshold defined by water supply and slope is exceeded. This is described by Montgomery and Dietrich (1988), who found that source area above a channel head decreased as slope increased, suggesting that in steep, humid landscapes, channels are initiated by land sliding. The relationship between source area and slope of channel initiation varies depending on local climatic and geological conditions. For the same slope, drier regions have larger source areas (Montgomery and Dietrich, 1988).

Where seeps occur in more gentle settings, channel initiation may be through overland flow where the amount of contributed water exceeds the storage capacity of the soils due to the presence of an underlying aquitard, resulting in surface flow. The resulting stream either occurs toward the centre of the wetland in a concave setting, or if slight sediment accumulation occurs in the middle of the wetland, the channel may form to the side.

In regions where subsurface lateral flows dominate the water source, it is possible to establish a relationship between duration and depth of inundation and the source area. In contrast, where the water is sourced primarily from fractures, bedding planes or faults in bedrock, the relationship between hydroperiod and source area is not consistent (Job and Le Roux, 2018). Channels that flow out of seep wetlands typically connect to the drainage network, and although of extremely low power, they do sporadically contribute to the downslope movement of colluvially derived sediment through land sliding in steeper areas, or surface flow sediment transport in more gentle areas.

ALLUVIAL WETLANDS

Floodplain Wetlands

The floodplain classification presented here is adapted from Kleinhans and Van den Berg (2011). Braided river floodplains have been omitted as they are rare in southern Africa, probably because there have been no recent glaciations in the region to support mechanical weathering processes required to provide large volumes of gravel and cobble sized sediment. Where stream powers are high enough to support the development of braided

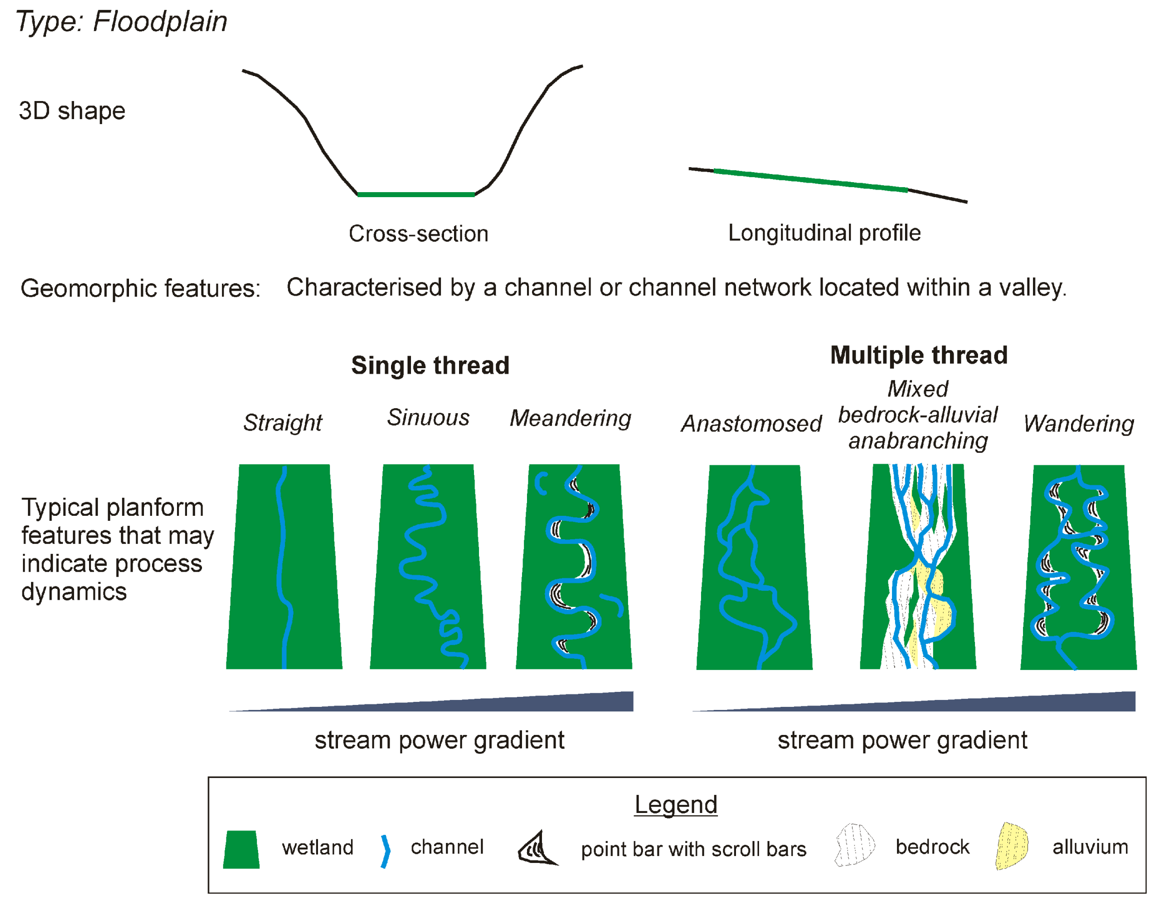


FIGURE 3 | Schematic shape and geomorphic features that are used to classify floodplain wetland type, followed by typical planform features that are used to classify sub-type.

TABLE 3 | Description of floodplain sub-types.

Macrotype	**Sediment source**	**Alluvial**					
Type	**Landscape position, shape, and geomorphic features**	**Alluvial floodplain**					
Sub-type	**Process dynamics (characteristic processes of erosion and deposition)**	**Straight river**	**Sinuous river**	**Meandering river**	**Anastomosed river**	**Mixed bedrock-alluvial anabranching river**	**Wandering river**
Description	**Floodplains:** Active erosion and deposition processes, number of active channels, and channel planform.	Laterally inactive, single thread, straight channel	Laterally inactive, single thread, sinuous channel	Laterally active, single thread, sinuous channel	Laterally inactive, multi thread, straight, or sinuous channel	Laterally inactive typically due to surface bedrock, multiple thread channel, ridge or irregular shaped islands	Laterally active, typically 2-3 threads, sinuous channel, features of meandering river floodplains common
Example wetlands and reference (if available)		Lotheni River, South Africa	Serpentine River, Wilderness, South Africa	Nsonge River (Grenfell M. C. et al., 2009), Klip River	Cooper Creek, Australia (Gibling et al., 1998)	Orange River, South Africa (Tooth and McCarthy, 2004)	Limpopo River, South Africa

Channels are arranged on an increasing energy gradient from straight to meandering for single-thread floodplain, and from anastomosed to wandering for multiple-thread floodplains.

rivers and there is a sufficient supply of bedload sediment, rivers are confined within a well-dissected drainage network developed in relatively erosion-resistant lithologies (e.g., basalt, dolerite, quartzite) or in lithologies that weather readily to sand, silt, and clay (sandstones, mudstones). Furthermore, braided river floodplains do not generally support edaphic environments suited to the widespread establishment of wetland vegetation—dynamic braidplains are characterised by low vegetation densities, as stable multi-channel networks are favoured where vegetation is sufficiently dense (Kleinhans, 2010). Floodplains may be classified into sub-types based on the presence of single or multiple channels, sinuosity, and evidence of lateral erosion and deposition (**Figure 3**, **Table 3**). In all floodplains, the dominant water input is from the channel and associated overtopping, while in some instances, lateral seepage from the valley sides may be important.

Channel pattern is indicative of the amount and size of bedload being transported, stream power, and channel stability (Kleinhans, 2010). As such, channel pattern should be considered along a morphological continuum that constantly evolves as conditions change. Large proportions of silt and clay increase floodplain cohesivity, and may therefore increase channel sinuosity. In contrast, as the proportion of fine sediment and vegetation is reduced, sinuosity decreases (Braudrick et al., 2009). The amount of sediment supplied to a channel, relative to stream power, may also have an effect on channel pattern; increasing sediment supply can result in braiding, whereas reducing supply can induce meandering (Church, 2006).

An increase in stream power relative to resisting forces of bed material calibre or bank material strength is typically associated with increased rates of lateral activity, such that for single thread channels, there is a continuum of form from low stream power (sinuous and straight, laterally inactive) to high stream power (meandering, laterally active; Nanson and Croke, 1992; Kleinhans and Van den Berg, 2011).

Anabranching rivers do not fit within low-energy meandering to high-energy braided planform continua (Kleinhans, 2010), and they generally have banks that are highly resistant to erosion, occur on extremely low gradients, and are often associated with mechanisms that block flow in the river channel, triggering avulsion (Nanson and Knighton, 1996). Nanson and Knighton (1996) divide anabranching rivers into six types, but for simplicity, we distinguish between three multiple-thread floodplain sub-types in this classification which may be distinguished by the degree of lateral activity, which is often indicative of dominant particle size and bank cohesivity.

Straight River Floodplain Wetland

Rivers that hold a straight planform for long distances are rare in nature, and tend to occur in headwater settings where valley confinement and supply of coarse material limit the efficacy of particle sorting processes, such that emergent alternate bars are not expressed in the planform (Parker, 1976; Kleinhans, 2010). Alternately, they may form where a channel has become set within the structural grain of an underlying fault, joint or fracture network (e.g., incision within the joint/fracture network of dolerite sills described by Tooth et al., 2002). Hydraulic instabilities in the flow, which are subsequently enhanced by alternate bar formation with sufficient sediment supply, tend otherwise to generate meandering (sand-dominated) or braided (gravel-dominated) channel patterns and associated floodplain features (Kleinhans, 2010). Riparian wetlands that flank straight channels are typically narrow, and derive from reworking of material transferred episodically through the system by hillslope-channel coupling (Harvey, 2001). Colluvial supply of material is therefore important, but the narrow floodplains that develop owe

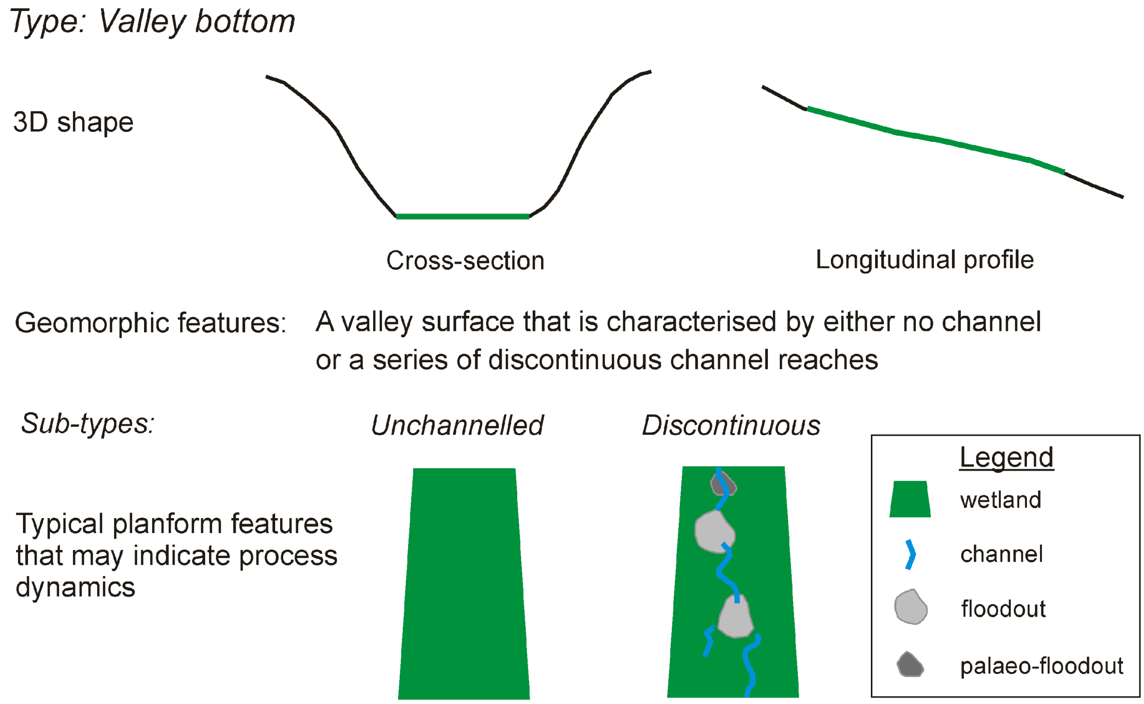


FIGURE 4 | Schematic shape and geomorphic features that are used to classify valley-bottom wetland type, followed by typical planform features that are process indicators used to classify unchannelled and discontinuous wetland sub-type.

their origin to the way in which colluvial material is reworked by the river channel. An example of a straight river floodplain wetland is along the foothills zone of the Lotheni River, South Africa (29° 27′ 10.72″ S, 29° 31′ 45.43″ E).

Sinuous River Floodplain Wetland

Sinuous river floodplain channels are characterised by a lack of active lateral migration, and are therefore devoid of typical active meandering river floodplain features like scroll bars, ox bow lakes, or meander scars. The lack of active meander migration in these systems may either be associated with low stream power, floodplain factors such as dense vegetation or a large proportion of fine sediment in the banks and channel bed, or planform ossification due to backwater effects. The attainment of high sinuosity is possible through very slow processes of bank collapse. A key distinguishing feature of stable sinuous and active meandering river floodplains (section Meandering river floodplain wetland) is the relative dominance of vertical accretion (overbank deposits) over lateral accretion. An example of a sinuous river is described by Tooth and McCarthy (2004) for some channels of the Okavango Delta, Botswana.

Meandering River Floodplain Wetland

Meandering rivers are sinuous, laterally active, single thread channels (**Figure 4**). Depending on the rate of lateral migration and sediment supply, an alluvial ridge is produced that elevates the channel and leveés above the floodplain. The characteristic migration of the channel across the floodplain results in the development of point bars and scroll bars, while old channel locations may be marked by ox bow lakes. Lateral accretion deposits (stacked point bars) dominate the sedimentary fill of meandering river floodplains. Backswamp areas of the distal floodplain environments may be substantially wetter than the alluvial ridge due to elevation differences. While the majority of meandering river floodplain wetlands receive most of their water from overbank flooding of the channel, they may also receive lateral valley inputs from tributaries, hillslope runoff, and seepage. Meandering river floodplains are sites of sediment exchange; their ability to act as sites of sediment storage depends on a variety of factors such as tectonic setting, rate of lateral migration and frequency of overtopping.

Key to meandering river dynamics is the integrity of lateral migration processes. River straightening, hardening or focussing flow through culverts can disrupt longitudinal sediment fluxes, resulting in channel incision and a reduction in overbank flooding. Excessive water abstraction either directly from or upstream of meandering river floodplains, such as for irrigation or mining, reduces stream power and may cause a meandering channel to switch from laterally active, to an inactive sinuous channel. Examples of meandering river floodplains include those of the Nsonge and Mfolozi rivers (Grenfell M. C. et al., 2009; Grenfell S. E. et al., 2009) and the Klip River (Tooth et al., 2002) in South Africa.

Anastomosed River Floodplain Wetland

Anastomosed rivers are characterised by low stream power, cohesive banks and low channel w/d ratios (Nanson and

TABLE 4 | Description of valley-bottom sub-types.

Macrotype	**Sediment source**	**Alluvial**	
Type	**Landscape position, shape and geomorphic features**	**Alluvial valley-bottom**	
Sub-type	**Process dynamics (characteristic processes of erosion and deposition)**	**Unchannelled**	**Discontinuous**
Description	**Valley-bottoms:** Active erosion and deposition processes, number of active channels, and channel planform.	No channel	In long profile, small reaches with channel, separated by vegetated floodout features. Deposition occurs on the floodout feature, but erosion occurs downstream at the reforming channel head.
Example wetlands and reference (if available)		Krom wetland (Pulley et al., 2018)	Northington, Hlatikulu, South Africa (Grenfell M. C. et al., 2009) and Nylsvlei, South Africa (McCarthy et al., 2011)

Croke, 1992). Channel sinuosity of individual branches varies. However, while occasionally highly sinuous, individual channel branches are laterally stable such that cut banks, point bars and oxbow lakes are generally absent (Makaske et al., 2002). Anastomosed floodplains typically occur where channel bed aggradation exceeds floodplain and leveé aggradation, driving channel avulsion (Nanson and Knighton, 1996; Jerolmack and Mohrig, 2007). In this classification system, an anastomosed river floodplain is akin to Nanson and Knighton (1996) type 1 or 2, where dominant sediment type can vary from mud to sand. An example of an anastomosing river floodplain is Cooper Creek in Australia (Gibling et al., 1998) and part of the Panhandle in the Okavango Delta, Botswana (Smith et al., 1997).

Wandering River Floodplain Wetland

A wandering river floodplain is characterised by multiple channels, typically 2–3, which are laterally active. In contrast to an anastomosing river floodplain, it is characterised by features of floodplain erosion and accretion (e.g., point bars, scroll bars, cut banks etc.) that are indicative of rapid lateral activity. They tend to have a higher stream power than anastomosing rivers, and in terms of sediment, they vary from mixed load to sand or gravel dominated (Nanson and Knighton, 1996). A wandering river floodplain encapsulates (Nanson and Knighton, 1996) type 3, 4 and occasionally type 5 floodplains. When gravel dominated, the channel pattern may vary from moderately braided to transitional between meandering and braided (Kleinhans and Van den Berg, 2011). Wandering river floodplains may either be the result of non-fluvial forcing (e.g., debris piles, reduction in flows) or disequilibrium dynamics (Kleinhans and Van den Berg, 2011). Many of the dry semi-arid to arid (UNEP, 1997 aridity index) South African floodplains are characterised by disequilibrium dynamics due to the impact of highly variable flows.

In dryland environments with variable flow regimes, these floodplains may support hydrophytic vegetation within the channel during periods of low or no flow. While the entire floodplain will be inundated during extreme flood events, certain types of wetland vegetation may withstand these floods to re-establish as flows are reduced. An example of a wandering river floodplain is the Touws River Floodplain in the semi-arid Karoo of South Africa (33° 37′ 48.62″ S, 20° 55′ 59.98″ E), and the Zambezi River Floodplain in Caprivi, Namibia.

Mixed Bedrock-Alluvial Anabranching Floodplain Wetland

This sub-type encompasses the ridge form and irregular sinuous anabranching rivers of Kleinhans and Van den Berg (2011), and is largely an outcome of episodically high stream power paired with resistant bedrock channel substrate and banks resulting in multiple channels. In addition to the occurrence of jointed/fractured granitoid outcrops which result in erosion resistant banks and islands, Tooth and McCarthy (2004) suggest that a variable flow regime may be an important factor in channel dynamics.

Channels are eroded preferentially along joints and fractures in the underlying bedrock. In order to accommodate variable discharge, multiple channels form around stable islands that may be composed of alluvium or bedrock. In low gradient reaches, sediment supply may exceed channel capacity, resulting in a surficial veneer of alluvial islands that becomes vegetated (Tooth and McCarthy, 2004), while small geomorphologically-transient palustrine wetlands may form in temporarily inactive channel branches. In steeper reaches, bedrock may outcrop more extensively as sediment transport capacity locally exceeds supply. An example of a mixed bedrock-alluvial anabranching floodplain wetland is that of the Orange River in the vicinity of Eksteenskuil, South Africa (Tooth and McCarthy, 2004).

Valley-Bottom Wetlands

Valley-bottom wetlands are those that occur on valley floors where a continuous channel is absent (**Table 4**, **Figure 4**). They are typically well-vegetated, fairly flat in cross-section and often perpendicularly abut large floodplain systems which act as a local base level control on incision. Valley-bottom wetlands are typically steeper and have smaller catchments than floodplain wetlands (Ellery et al., 2016). We discern two main sub-types; an unchannelled valley-bottom and a discontinuous valley-bottom. Geomorphic processes of the latter are better documented, and in general, an improved understanding of the development of unchannelled valley-bottoms is required.

In the southern parts of the Western and Eastern Cape of South Africa, where valley-bottom wetlands have formed due to repeated cycles of cutting and filling (Pulley et al., 2018), the gradual release of groundwater onto the valley floor from adjacent highly folded and fractured mountain landscapes sustains low flows along the valley floor (Tanner et al., 2018). Given this pattern of inputs, flows are sustained but typically low, with low stream power, such that the valley-bottom wetland remains wet for long periods.

Discontinuous Valley-Bottom Wetlands

Discontinuous valley-bottom wetlands are characterised by short reaches of stream channel, separated by patches of aggradation in floodout features. However, floodout features may not always be very well-developed, or may not be visible due to vegetation cover. The channel is deepest at the wetland head, where it may be actively eroding, and becomes progressively shallower downstream until it loses confinement completely and deposits sediment on a prograding fan. Sediment deposited on the floodout fan fines toward the distal reaches. Channels tend to reform toward the base of the fan due to localised steepening. In some cases, tributary streams may locally increase capacity and competence, resulting in reforming channel initiation (e.g., Nylsvlei, McCarthy et al., 2011). Due to the complexity of the local topography, the hydroperiod of such wetlands is varied, with the wetland close to the floodout apex generally experiencing the wettest conditions. Frequency of inundation depends on local rainfall patterns as groundwater contributions, except from lateral seepage, are usually limited.

Discontinuous valley-bottoms have been comprehensively described in a variety of climatic settings. In some settings the formation of fans appears to be linked to the localised effect of resistant lithology, while in others, no geological control was found (Grenfell M. C. et al., 2009; Grenfell et al., 2012, 2014). There is evidence to suggest that at millennial timescales, sediment fill in some valleys is almost completely evacuated by gully incision and widening. In Australia, Fryirs and Brierley (1998) documented three phases of erosion and two phases of infilling in just 6,000 years, suggesting that these wetlands are particularly dynamic. The landscape in such a system may be considered to have two alternate transient states. In one state, the valley is completely eroded with no sediment infill and during this phase, the bedrock valley floor is eroded. In the second state, ongoing erosion upstream produces a pulse of sediment that accumulates on the valley floor, eventually producing a substantial valley fill upon which localised streams and floodouts slowly disperse sediment downstream. It is not known over what time scales these processes naturally operate in different dryland environments, although it is known that human settlement can accelerate incisional processes (Brierley and Fryirs, 1999).

This process was also documented in wetlands dominated by *Prionium serratum* (Palmiet), where it was found that successive phases of gully incision were initiated in response to gradual steepening by aggradation, and led to a reduction of valley slope (Pulley et al., 2018). In the case of discontinuous valley-bottom wetlands, intrinsic controls on slope and patterns of sedimentation force the system to evolve toward a threshold. Despite evidence for self-organised criticality, these systems are extremely vulnerable to human induced changes to catchment water and sediment supply, typically created through changes in land use or invasion of alien plants (Rebelo et al., 2015). When restoring such wetlands, it is essential that the original cause of change to catchment patterns of sediment and water supply is addressed. Furthermore, interventions must be sensitive to lateral and longitudinal sediment connectivity, as preventing the downstream migration of sediment may cause erosion elsewhere.

Unchannelled Valley-Bottom Wetlands

Unchannelled valley-bottom wetlands are typically well-vegetated wetlands located on the valley floor, characterised by a lack of surficial geomorphic features. Flow across the wetland is diffuse, although there may be localised flow paths within or even underneath vegetation. The lack of channel development, despite a steeper valley slope than most floodplains, is likely related to low stream power, which may be further reduced by the effect of dense vegetation. These wetlands are typically permanent or seasonal, with temporary zones located laterally along the valley side. Water inputs are derived from rainfall, upstream channels and lateral and longitudinal seepage, whether from inter-flow or groundwater sources.

Care should be taken when classifying unchannelled valley-bottom wetlands, as they may actually be blocked-valley wetlands, especially when abutting a large alluvial floodplain, or they may be geochemical depressions. A true unchannelled valley-bottom wetland would be longitudinally connected to downstream systems, and would not be a depression.

As unchannelled valley-bottom wetlands are connected to the drainage network, they must undergo phases of erosion such that the valley floor may be constantly lowered (e.g., Pulley et al., 2018). In terms of long-term geomorphic processes, they must occasionally undergo phases of incision similar to those of discontinuous valley-bottom wetlands. The main contrast appears to be related to local processes of sedimentation. Within unchannelled valley-bottom wetlands, sediment supply appears to be extremely low. Incoming sediment is filtered evenly across the wetland, resulting in a homogenous wetland surface. The lack of localised aggradation processes prevents local steepening and channel formation, allowing patterns of diffuse flow to be preserved. Nevertheless, extremely slow sediment accretion that occurs preferentially toward the wetland head results in gradual steepening of the wetland, until a critical threshold is reached. Under natural conditions, it can be assumed that the complete cycle of aggradation and incision must be slower than that of discontinuous valley-bottom wetlands, where the turnover rate is higher.

These wetlands are extremely vulnerable to interventions that focus flow patterns (e.g., road culverts) and locally increase stream power, causing erosion. In addition, changes to catchment land use may alter water and sediment supply to the wetland, potentially enhancing processes of aggradation (due to increased sediment supply) or causing erosion (due to an increase in peak run off).

Blocked-Valley Wetlands

Blocked-valley wetlands occur along valley floor reaches and can be fairly extensive longitudinally (**Figure 5**). They are formed

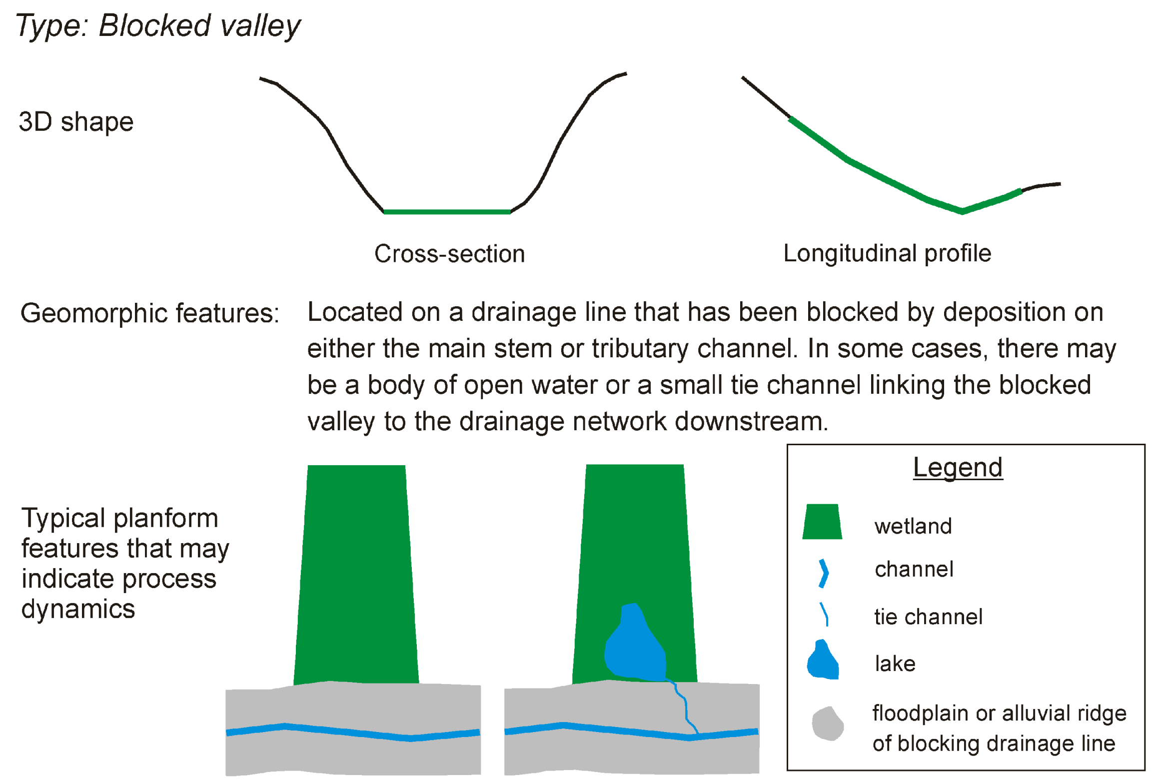


FIGURE 5 | Schematic shape and geomorphic features that are used to classify blocked-valley wetland type, followed by typical planform features that may or may not occur.

along drainage lines where rates of aggradation on one confluent channel exceed that of the other confluent channel, leading to valley impoundment, the impediment of water and sediment flows, and lake or wetland formation. Blocked-valley wetlands may form in tributary or trunk valleys, but in either case the confluent channel driving impoundment has a higher sediment load. This may be due to a larger catchment area, discharge and sediment supply, as is the case when a tributary is blocked by the trunk channel (e.g., Grenfell et al., 2010; Ellery et al., 2012). In other cases the larger sediment load may be attributed to differences in land use, land cover, soil, geology or slope (e.g., Joubert and Ellery, 2013).

Due to their specific landscape setting, blocked-valley wetlands are characterised by particular patterns of sediment accumulation and hydroperiod (Grenfell et al., 2008, 2010). As stream power is reduced by a rising local base level, sediment begins to accumulate in the depression. Sediment typically fines downstream and if the catchment is sufficiently wet, peat may accumulate in the lowermost area of the valley if it is permanently waterlogged (Ellery et al., 2012). Depending on the relative difference in aggradation rate as well as the local climate, the resulting depression may have an area of open water which is too deep for colonisation by emergent macrophytes. Blocked-valley wetlands and lakes occur in dryland settings as well as more humid environments, as typified by Lake Murray on the Strickland River in Papua New Guinea. These wetlands are vulnerable to rapid infilling due to a change in upstream catchment activities (e.g., removal of native vegetation), as well as increases in abstraction of water in the catchment (e.g., plantations) and from the wetland itself for irrigation.

Wetland Plain

Wetland plains, described by Ollis et al. (2015) as “flats,” are extensive systems with no distinct local topography (**Figure 6**) that typically form on coastal plains. Due to the extremely low gradient, flow is diffuse, and processes of sediment transport are considered minimal. As they are not linked to stream flow, and are not fed by local catchments, water is primarily derived from local rainfall although there is potential for rising primary aquifer levels to locally intersect the land surface. In terms of geomorphic features, wetland flats may be characterised by isolated depressions. There have been no significant publications on geomorphic characteristics of wetland flats in southern Africa, and this description remains largely untested. Wetland plains often occur as part of a complex mosaic of wetlands that include floodplains, fans, depressions, and valley-bottom wetlands. It is likely that due to climatic constraints, wetland plains in drylands are highly variable in extent, and have largely seasonal or temporary hydroperiods. Portions of the Agulhas wetland system surrounding Prinskraal, Western Cape, South Africa are an example of alluvial wetland plains (see **Figure 1**).

Wetland Fan

Alluvial fans form at locations of loss of confinement as a stream discharges onto a receiving basin of very low gradient. Alluvial fans are well-known in arid environments as being generally

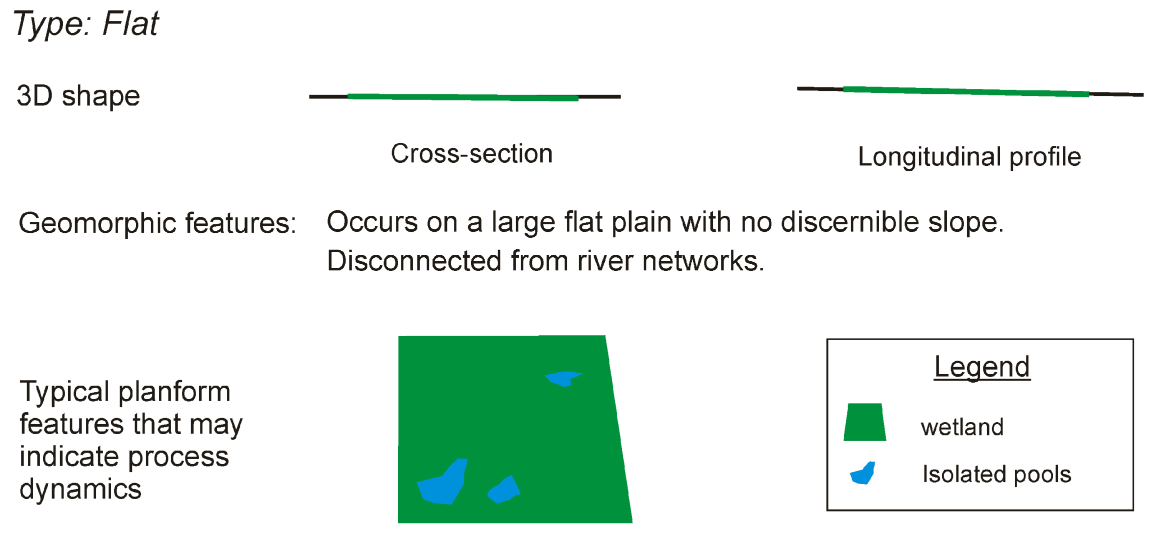


FIGURE 6 | Schematic shape and geomorphic features used to classify a flat type wetland, followed by typical planform features.

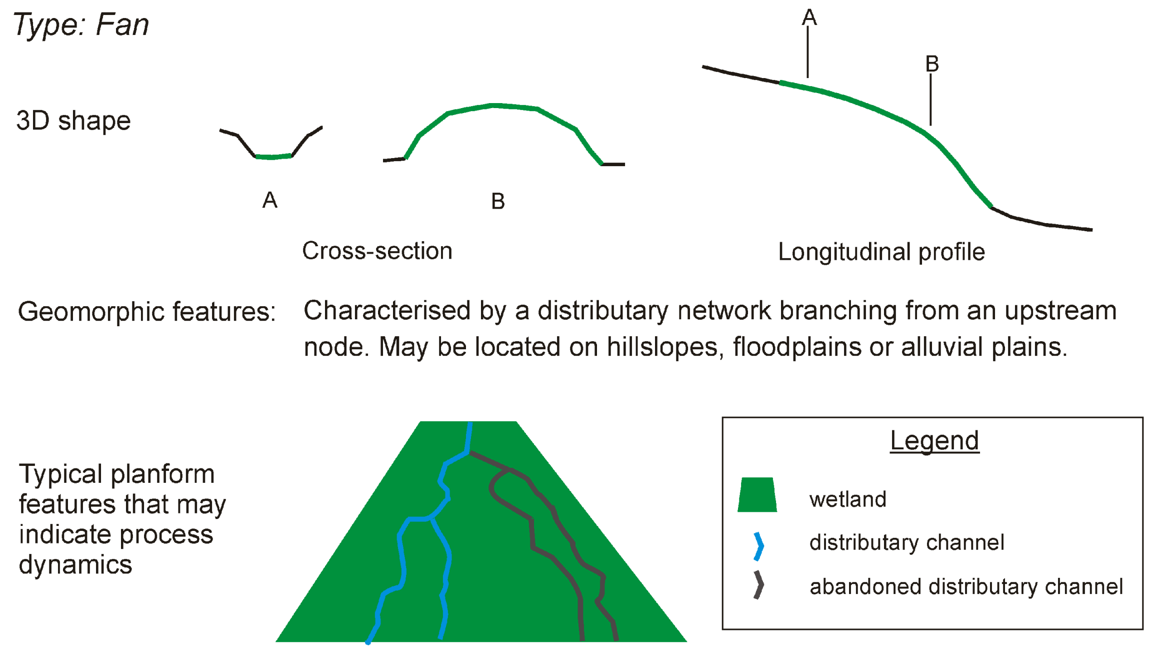


FIGURE 7 | Schematic shape and geomorphic features that are used to classify a fan type wetland, followed by typical planform features that may or may not occur.

devoid of hydrophytic vegetation, although the Okavango Delta is strictly an alluvial fan with a large area that is permanently flooded and densely vegetated (McCarthy et al., 1988, 1997, 2002; Stanistreet et al., 1993). In the case of the Okavango Delta, a large river drains a catchment with high rainfall and discharges into a rift valley basin oriented perpendicular to the watercourse in a semi-arid setting (rainfall $< 500\,\text{mm.a}^{-1}$). Wetland alluvial fans are fairly common in dry sub-humid and semi-arid areas of South Africa, and vary quite substantially in terms of size. They may also form in a variety of landform contexts, including valleys, plains or hillslopes. Fans are conical shaped sediment deposits that occur when a stream loses confinement at the apex, resulting in adjustments to stream width-depth ratio and concomitant deposition (**Figure 7**). Loss of confinement is generally controlled by geological factors, such as rifting (McCarthy et al., 1997) or a change in lithology, or may simply be due to a landform transition such as confined tributary valley to unconfined trunk floodplain.

Unlike a discontinuous valley-bottom wetland, fans are standalone features and are not associated with a cascading system of floodouts and reforming channels. However, they are similar to floodouts in discontinuous valley-bottom wetlands in terms of sedimentology and hydroperiod. Fans are characterised by sediment fining from the apex to distal reaches, and have a network of distributary channels, some of which may be abandoned and some of which may be morphodynamically active. Fans are dependent on surface water and sediment inputs, and if deprived of these the wetlands may become incised and desiccate. Depending on climatic and/or inflow regime, fans may be permanently wet or, in more arid environments, seasonally or temporarily wet (e.g., Grenfell et al., 2012).

AEOLIAN WETLANDS

Aeolian Depression Wetlands

Aeolian depressions, frequently called pans, form in paleaolacustrine basins, and on palaeodrainage lines, interdunes, and coastal plains (Goudie and Wells, 1995). For pans to persist, the setting of formation must be largely isolated from current fluvial activity, while aeolian sediment sources and fluxes should not be so overwhelming that hollows are rapidly infilled. Most pans are not a product of aeolian deflation alone, but also require the action of salt weathering (Goudie and Wells, 1995).

The majority of depressions that are not located in dune fields form on lithologies that are vulnerable to salt weathering. In general, rocks formed in marine environments are more susceptible as weathering liberates salts which may then exacerbate rock disintegration by crystallisation and hydration. Once the rock has been weathered the individual grains that have been liberated are removed by wind erosion. In southern Africa, animals using the resultant pan as a waterhole can enhance deflation processes (Marshall and Harmse, 1992).

Pans are typically ovoid or cuspate in shape, with a lunette dune downwind of the pan. In areas where salt weathering is important, the pan is typically only seasonally or intermittently inundated. Hydrological inputs are usually derived directly from precipitation. Aeolian depressions are vulnerable to changes in local land use that increase sediment availability and result in infilling. An example of typical aeolian depressions are those of the Northern Cape pan belt, South Africa (Goudie and Wells, 1995).

GEOCHEMICAL WETLANDS

Geochemical Depression Wetlands

Geochemical depression wetlands typically form in valley or plain settings where permanent saturation of underlying bedrock chemically alters and simplifies the mineralogical composition, resulting in a loss of mass and volume. Geochemical depressions may be divided into four sub-types; subsidence depressions formed on igneous rocks, redox depressions formed by redox reactions as a result of repeated cycles of wetting and drying, dissolution depressions formed on karstic rocks such as limestone or dolomite and margin-aggradation depressions formed by precipitation of allochthonously introduced solutes in the pan margin (**Table 5**). While karstic depression wetlands are dissolution features, igneous depression wetlands are features of hydrolysis, resulting in different characteristic geomorphic and hydrological features. Based on the Ollis et al. (2015) hydrogeomorphic classification, many geochemical depression wetlands would be classified as valley-bottom wetlands due to their appearance in aerial photography. However, their underlying stratigraphy is entirely produced by chemical weathering of bedrock rather than by reworked fluvial sediment, typically covered by a superficial peat deposit if local hydroclimatic conditions allow. Geochemical depression wetlands are particularly vulnerable to changes in catchment hydrology (e.g., increased run-off, reduced infiltration) as saturation is often fundamental to the geochemical processes required for their formation.

Subsidence Depression Wetlands

Subsidence depression wetlands are generally formed where the underlying bedrock is igneous and has a substantial proportion of feldspar, although they have been recorded on tillite with a high proportion of feldspar. When permanently saturated with slightly acidic water, feldspar minerals are simplified by the loss of metals such as iron, calcium, magnesium, and sodium to form clay minerals such as kaolin. In the case of Edwards et al. (2016), feldspar minerals in a dolerite sill were transformed through hydrolysis to kaolin. The *in situ* formation of saprolite results in surface sagging, which creates a basin and promotes inundation and wetland formation. Prolonging inundation acts as a positive feedback, as saturation enhances hydrolysis.

These wetlands are surprisingly common on ancient land surfaces such as the African erosion surface in southern Africa, which has weathered for in excess of 60 million years (Holmes and Meadows, 2012). This suggests that prolonged weathering is required for their formation, which is likely to be in the order of 1 mm per 10,000–20,000 years (Edwards et al., 2016). These systems vary considerably in inundation duration, from being permanently to seasonally or ephemerally inundated. In the case of Edwards et al. (2016), prolonged saturation occurred following development of a meandering river floodplain on resistant dolerite. The resultant wetland is therefore characterised by meandering river features such as abandoned meanders. However, due to internal sagging, the river is no longer laterally active. Igneous depression wetlands may therefore have characteristics of depression wetlands (e.g., isolated water bodies) as well as relic features of old landscape processes (e.g., channels). Water inputs are dominated by surface channel flows and diffuse runoff, although seepage might be locally important. Due to the formation of a depression, most of the incoming sediment may be trapped within the wetland during low or mean flows.

Redox Depression Wetlands

In contrast to subsidence depressions, redox depressions are formed in seasonal climates, where there are repeated cycles of wetting and drying. During the wet season, Fe^{3+} is converted to the more soluble ion Fe^{2+} by reduction of the underlying soil and bedrock in anaerobic conditions. Vegetation transpiration on the depression edges draws water toward the depression margins, moving the soluble Fe^{2+} away from the depression centre. During the dry season, the wetland is exposed to oxidising

TABLE 5 | Geochemical depression sub-types.

Macrotype	**Sediment source**	**Geochemical**			
Type	**Landscape position, shape and geomorphic features**	**Geochemical depression**			
Sub-type	**Process dynamics (characteristic processes of erosion and deposition)**	**Subsidence depression**	**Redox depression**	**Margin-aggradation depression**	**Dissolution depression**
Description	**Geochemical depressions:** Substrate type and/or whether solutes are allochthonous or autochtonous.	Typically located on igneous rocks (e.g., basalt or dolerite) that have been weathered by hydrolysis due to permanent saturation. The depression is created by consequent sagging as the minerals are reduced in volume. Autochtonously derived minerals.	Formed by repeated movement of metal ions toward the wetland margins through redox reactions as a result of repetitive cycles of wetting and drying. Autochthonously derived minerals.	Initial substrate is typically alluvium, to which solutes are allochthonously supplied. Local evapotranspiration processes enhance solute concentrations, causing precipitate formation.	Located on carbonaceous rocks such limestone or dolomite, may be linked to groundwater through an underground cave network (e.g., dolomitic eye). The depression is created by sagging as underlying rocks are dissolved by circulating groundwater.
Example wetlands and reference (if available)		Dartmoor Vlei (Edwards et al., 2016)	Shadow Vlei (Ellery, 2019)	Pans in the Okavango (McCarthy et al., 1993)	Ephemeral pans in the Namib (Marker, 1982)

conditions in an aerobic environment. This transforms the ions to insoluble $Fe^{3+,}$ which then comes out of solution on the depression margins, where it builds local relief. Over a prolonged period of time, repeated cycles of wetting and drying result in a loss of volume in the centre of the depression, with concomitant aggradation on the margins.

This process may be fairly common on ancient erosion surfaces that have been exposed to weathering processes for long periods of time. First described by Ellery (2019) for Shadow Vlei, in the Eastern Cape of South Africa, the resultant depression is surrounded by a ferricrete rim that is slightly elevated above the surrounding landscape. The same process can also result in the development of calcrete rims (Alistoun, 2014).

Margin-Aggradation Depression Wetlands

In contrast to redox depression wetlands, the soluble ions responsible for relief building in margin-aggradation depression wetlands are not derived *in situ*, but are supplied allochthonously by circulating waters rich in solutes. The archetypal example of a margin-aggradation depression is described by McCarthy et al. (1993) for the interior of alluvial islands on the Okavango Delta. Large, deep-rooted trees grow preferentially on the island margins, and are responsible for increasing groundwater salinity, leading to saturation of calcite and silica, by transpiration. Sub-surface saturation results in precipitation of calcite and amorphous silica, leading to vertical expansion on island margins. The creation of topographic relief on the margin creates a central depression, characterised by sparse, salinity tolerant vegetation. On older islands, vegetation in the depression may be replaced with sodium carbonate deposits. In contrast to the long time frames required for the formation of subsidence and redox depressions, numerical modelling suggests that salinisation of the groundwater occurs over timespans between 100 and 200 years, but that aggradation of island margins takes place over much longer timespans. The formation of margin-aggradation depression wetlands requires specific hydroclimatic conditions, such as low annual precipitation to allow local saturation of groundwater, as well as reliable surface water inflows.

Dissolution Depression Wetlands

Dissolution depression wetlands occur in areas underlain by water soluble and porous carbonate rocks and are synonymous with typical karst landscape features such as swallow holes, disappearing streams and solution sinkholes. Wolfe (1996) described two types of dissolution wetlands of karst landscapes, karst pans and compound sinks, which differ in terms of their degree of connection to the groundwater drainage system. Karst pans are very shallow with no direct connection to groundwater. They are formed due to subsidence as the underlying calcareous rocks are dissolved. In some cases, they may be lined with clay, effectively sealing the base of the wetland to groundwater losses (Greear, 1967). In contrast, compound sinks are deeper and linked to the underground drainage network. As a result, sources and patterns of water inputs to karst depressions are highly varied. O'Driscoll and Parizek (2003) found that sinkhole wetlands in Pennsylvania, USA were fed primarily by direct precipitation as well as a perched groundwater table. As a result, dissolution depression wetlands may be seasonal (e.g., Kobza et al., 2004) or permanently inundated. For simplicity, we do not further subdivide dissolution depression wetlands. Dissolution features and the resultant ephemeral wetlands similar to those described above have been described in the Namib by Marker (1982).

DISCUSSION

While the classification is based primarily on research from southern African wetlands, it is clear from the large and growing literature on wetlands in drylands across the globe (see further examples from Africa, Australia and southwest USA in Lisenby et al., 2019) that many of the processes described occur in other dryland environments, as well as in humid environments where wetlands are created by process-form feedbacks. The classification is physics-based and determined by processes of sediment deposition and erosion which apply globally, and it is therefore anticipated that the classification approach presented may be more widely applied and expanded than currently detailed.

Wetland types that have not previously been defined with reference to a clear process-based mode of formation have been excluded (e.g., channelled valley-bottom wetlands, where there is no compelling geomorphic reason to distinguish these features from floodplain wetlands at a high level in classification; Nanson and Croke, 1992), and where necessary, sub-types have been provided such that wetland forming processes may be better contextualised and understood. The advantage of this classification system is that all modes of dryland wetland formation identified in the literature are included. As research advances, additional wetland types may be added in accordance with the discriminatory framework developed. The implications of the genetic classification system for understanding spatial and temporal variability in form and process of wetlands in drylands are discussed in the sections that follow.

Fluvial Wetlands and Alternate Transient States

Dryland wetlands are highly dynamic ecosystems, developing under extreme climatic conditions that are often characterised by alternating phases of floods and droughts. This, in combination with their frequent occurrence on drainage lines, results in wetlands potentially shifting between alternate stable states (e.g., Rountree et al., 2001). While some wetlands may be quite resilient to environmental change (Tooth, 2018), geomorphic processes in others result in alternation from one state to another. When classifying wetlands and developing catchment management plans, it is useful to be aware of the different forms that a wetland may take over time, and to consider the temporal scale at which such change takes place.

Over short time scales (seasons to years), if we consider a non-perennial river that flows seasonally or intermittently, during periods of no flow the river becomes akin to a discontinuous valley-bottom wetland with a series of disconnected pools and reed beds. However, during flood events, the entire floodplain may become a macro channel for flow. There are thus two alternate transient states for this system depending on flow conditions.

On a geomorphological time scale (centuries to millennia), two prevailing geomorphic misconceptions (Schumm, 1994) are frequently applied to dryland wetlands, potentially because they are often viewed exclusively as ecosystems rather than also as geomorphic systems. For many ecologists, wetlands represent a stable habitat that supports obligate species that are adapted to that environment. The assumption is that the particular biophysical conditions that support those species have existed for a very long time. Thus, for many wetland scientists, there is a perception of stability, which supports an underlying view that any adjustment to a wetland ecosystem must have been caused by humans. However, when we consider valley-bottom wetlands as geomorphologists, it is clear that for a drainage line to exist, it cannot always have been a site of aggradation.

Contrastingly, once a wetland has entered a state of erosion, whether anthropogenically-forced or otherwise, there is a perception that the adjustment will never cease, and that the wetland will not recover unless intervention occurs. This is (Schumm, 1979) misperception of instability. However, cut and fill landscapes are driven by geomorphic threshold behaviour, where self-reinforcing, continuous but gradual changes (e.g., in longitudinal slope, associated with ongoing aggradation) force an abrupt switch in system behaviour (to incision; Ellery et al., 2016). Aggradational processes within valley-bottom wetlands result in oversteepening over the long term, and once a geomorphic threshold is reached, they begin to erode. When the gullies are completely connected, the valley fill is completely or partially evacuated. The sudden availability of sediment overwhelms the drainage line downstream, causing aggradation, the effects of which cascade up- and downstream (**Figure 8**). The valley-bottom wetland therefore oscillates between gullied and wetland states (Grenfell M. C. et al., 2009; Ellery et al., 2016; Pulley et al., 2018). While natural aggradation can force the system toward a critical threshold, external factors that enhance aggradation within the wetland, or increase the frequency and magnitude of catchment runoff supply, can artificially accelerate the process.

Integrating Spatial and Temporal Process Scales

Due to the wide variety of spatial scales at which geomorphic processes occur, it is possible for wetland types to be spatially nested within each other. This does not undermine the concept that it is the mode of formation of each wetland that is important, but rather supports the system-scale view that processes may operate at different spatial scales (Fryirs et al., 2018). For example, the Okavango Delta is a large wetland system that has formed on a graben structure in Botswana. The system as a whole may be classified as an alluvial fan as it has formed as a result of loss of confinement (**Figure 9A**). However, if we consider the wetland at finer resolution, we may also characterise different types of floodplain which have formed due to variations in flow and sediment transport (**Figures 9B,C**). On the distal reaches of the alluvial fan, geomorphic processes are extremely different, and geochemical depression wetlands occur due to evapotranspiration and subsequent solute enrichment (**Figure 9D**). Understanding and illustrating the nested hierarchies of process and form that characterise many large wetland systems provides essential insight into wetland structure, function and dynamics, but is also an essential tool for communicating this insight in management initiatives (Dollar et al., 2007; Fryirs et al., 2018).

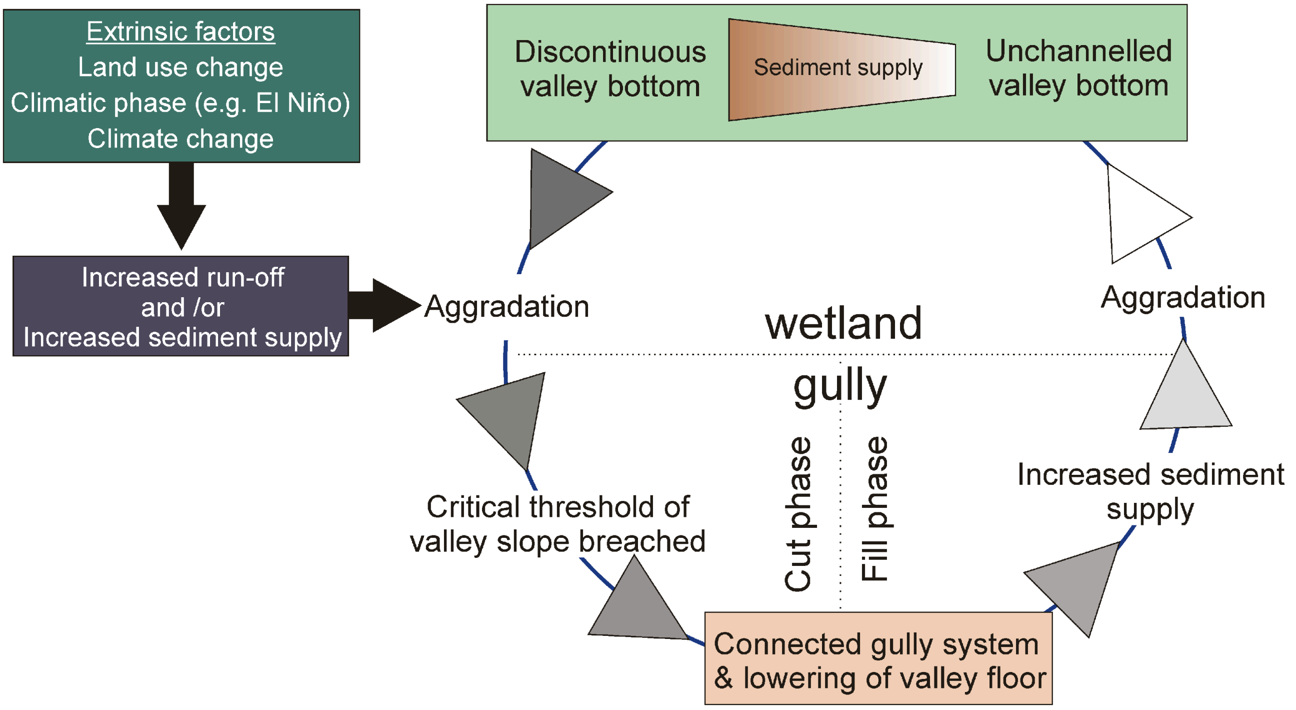


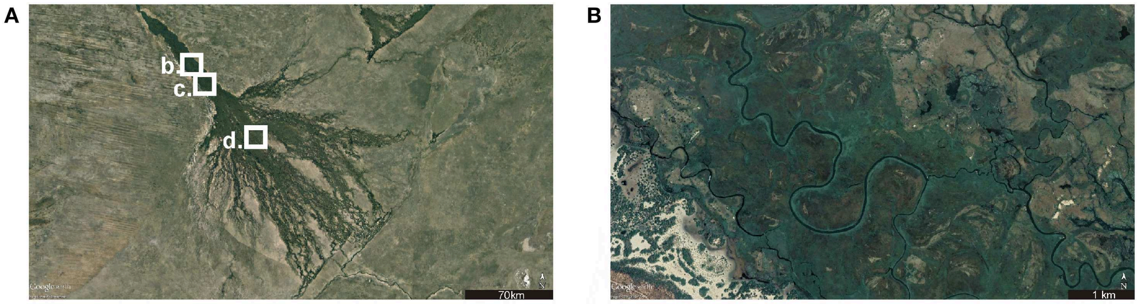
FIGURE 8 | In an example of self-organised criticality, aggradation in valley-bottom wetlands results in valley steepening. Ongoing aggradation eventually results in incision once a particular valley slope threshold is breached. The release of valley fill sediment through erosion causes aggradation downstream, eventually resulting in the formation of new valley-bottom wetlands. Whether the wetland is a discontinuous or unchannelled valley-bottom wetland may be related to catchment sediment supply during the fill phase, with discontinuous systems being characterised by a larger sediment supply.

Similarly, geomorphic processes may operate at varied temporal scales. In floodplains, an individual flood event may shape an in-channel bar or set of bars, while long term channel migration and development of an alluvial ridge may occur within decades or centuries (**Figure 10**). Geomorphic diversity and variation in wetland habitat in such systems arises over time through the interplay of processes that occur relatively gradually and continuously (e.g., channel lateral migration toward a backswamp environment), and processes that occur abruptly, though perhaps after a lengthy period of initial development (e.g., intersection of meander necks forming an oxbow lake, or avulsion following headward incision that intersects a low point in the channel upstream). Morphological changes in alluvial fans may also be fairly abrupt, with channels switching course following natural aggradation. Where material fluxes are more diffuse, geomorphic processes tend to occur more slowly. For instance, many aeolian and geochemical depressions in southern Africa are located on ancient erosional surfaces. The formation of these wetlands potentially takes place over tens-to-hundreds of thousands of years. Understanding the typical timescales over which different features within wetlands are formed is critical to our interpretations of change, and to distinguishing natural changes from those that may have been anthropogenically accelerated. It is also critical to understanding the natural recovery potential of wetlands, in determining the time required for natural recovery to progress in a particular geomorphic setting if/once the cause of degradation has been removed.

Implications for Understanding Geomorphology, Sediment Fluxes, and Ecosystem Service Provision

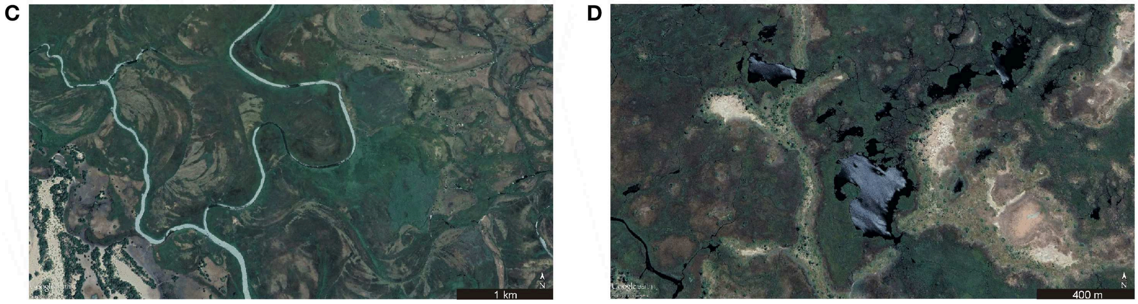
A re-envisioning of what constitutes a functional wetland unit and acknowledgment of system-scale linkages between wetlands and catchments is essential for successful wetland restoration in dryland environments. In the genetic classification system presented here, the wetland is an integrated system with characteristic local fluxes of water and sediment. A wetland classified according to its mode of formation may encompass several hydrological zones, although the wetland type and sub-type may provide an indicator of the typical spatial arrangement and temporality of those zones. This is in contrast to Semeniuk and Semeniuk (1995) and Ollis et al. (2015), where the functional unit is a combination of a hydrogeomorphic descriptor or type and the hydrological regime. The main aim of the genetic classification system is to provide insight into characteristic patterns of landform development, which generally arise through sediment entrainment, transport and deposition.

For dryland wetlands, understanding the manner in which sediment moves through the landscape is essential. This often requires a catchment scale understanding of sources of sediment supply, and the likely impact of changes in land use or treatment. Changes in run-off, either through physical abstraction, land use change or alien plant infestation, may also influence river capacity and competence, either increasing



Alluvial fan wetland

Sinuous river floodplain wetland



Anastomosing river floodplain wetland

Margin-aggradation depression wetland

FIGURE 9 | Wetland types and their associated processes and dynamics may be nested. For example, the Okavango Delta is an alluvial fan in a tectonic setting **(A)**. On the panhandle, different types of floodplain wetlands occur due to downstream variation in sediment supply and discharge regime **(B,C)**. In the fan region, tree-fringed geochemical depressions occur **(D)**. All images from Google Earth.

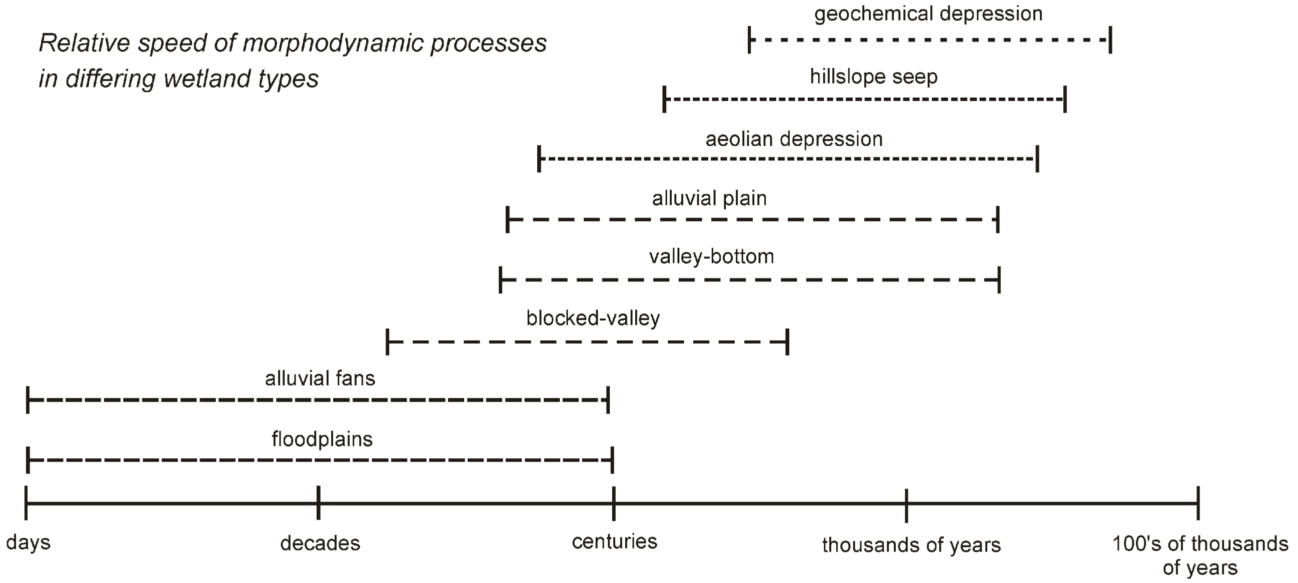


FIGURE 10 | A comparison of relative speed of typical morphodynamic processes in different wetland types.

it if flood peaks are enhanced, or reducing it if abstraction rates are high. The proposed genetic classification of wetlands acknowledges that the maintenance of sediment supply may be as important as water supply in these wetlands, and is essential for maintaining biodiversity and ecological processes (Wohl et al., 2015).

Processes of sediment transport and deposition, their magnitude, and their temporal and spatial scale have implications for two tasks common to wetland practitioners; (a) planning of wetland restoration projects, and (b) assessments of wetland ecosystem services. When considering the rehabilitation of an eroded wetland at the functional unit scale that has previously been used in South Africa, it is perhaps easy to overlook geomorphic processes that occur throughout a drainage line, and which are vital for maintaining and creating wetlands downstream. At a local scale, preventing further headward erosion and encouraging the deposition of sediment is useful as it allows wetland processes on site to be maintained. However, for downstream systems, dependent on an upstream sediment supply, artificially reducing longitudinal connectivity (i.e., through a weir or other barrier to sediment movement) can be catastrophic (e.g., Kondolf et al., 2006). In a wetland that is actively aggrading, such as in some floodplains and all valley-bottom wetlands, a reduction in sediment supply may result in erosion, effectively reversing the system into a cutting cycle. It is vital that drainage line wetlands are considered holistically in terms of both water and sediment connectivity such that meeting the immediate aims of local restoration does not cause harm downstream in the future. Even in systems which have been subject to aggradation as a result of anthropogenically-enhanced catchment sediment supply, have crossed a threshold slope (Ellery et al., 2016), and are undergoing incision, it must be acknowledged that this represents a system level reorganisation of material that will in time self-organise wetland development through the drainage network. In this case, the forced retention of sediment at discrete points in the network using engineering structures is in fact working against these natural processes. Greater attention should be paid to identifying the cause of degradation, and the persistence of degrading forces within the system, so that restoration efforts can work with natural processes to enhance natural recovery.

Since the genetic classification system for palustrine wetlands in dryland settings offers an improved conceptualisation of sediment movement, it is anticipated that there will be an improvement in understanding of the provision of ecosystem services, especially with regards to services associated with sediment trapping, assimilation of nutrients, and the removal of contaminants and toxicants. For instance, floodplain wetlands are often considered excellent at sediment trapping (e.g., Kotze et al., 2009), but for many dryland wetlands, inundation of the floodplain due to overbank flooding may be infrequent. As such, in dry years, floodplain wetlands which experience some lateral migration but limited overbank connectivity are likely to be net exporters of sediment. Furthermore, the vertical growth (i.e., depth of sediment storage) of the floodplain is limited by processes that can result in a net return of sediment from the floodplain to the channel (described by Lauer and Parker, 2008), either through scour during extreme floods, bank slumping or meander migration. Further research is required in dryland floodplain settings to determine actual rates of sediment trapping efficiency. In contrast, blocked-valley wetlands are extremely effective at trapping sediment and associated contaminants, as the entire sediment supply is likely to be trapped, while water may still seep down valley. The classification system also offers an enhanced understanding of sorting processes that lead to spatial variation in sediment and nutrient dispersal within wetlands. Nutrient/toxicant uptake in wetlands (especially the sediment associated/adsorbed component) depends as much on their input spatial distribution, as it does on the biogeochemistry of plant or bacterial uptake processes, and this input spatial distribution is conditioned by advective and diffusive geomorphic transport processes (e.g., material fining with increasing distance from a channel margin or terminus).

CONCLUSION

The proposed genetic classification system offers a complementary approach to several existing vegetation-based or hydrogeomorphic classification systems when applied for the purpose of wetland management or rehabilitation planning. The classification structure lends itself to additions that could expand the classification globally and ensures that when applied consistently, a wetland may fall into only one class. However, it is flexible in that when considered at increasing resolution, additional wetland types may be nested within larger systems.

The main conceptual difference from existing classification systems is that the characteristics of the sediment flux are explicitly included, which results in a classification system that is truly responsive and inclusive of geomorphic processes responsible for the formation and ongoing existence of wetlands in drylands. It encourages holistic consideration of wetland systems and recognises that fluxes in sediment and water occur both longitudinally and laterally within wetlands, and that this is important for the long-term viability of wetlands when comparing management or intervention options.

Furthermore, by more accurately detailing geomorphic processes occurring within wetlands, our ability to predict changes associated with altering sediment or water flux in the catchment and within the wetland is improved. It is anticipated that application of the genetic classification approach will encourage a landscape approach to wetland management, where wetlands are understood to be components of an integrated catchment. This is especially important in dryland settings as the frequent occurrence of wetlands on drainage lines makes them vulnerable to changes in catchment land use that impact upon downstream flood peaks and/or sediment supply. It is hoped that use of the genetic classification system will provide information required for the development of catchment management plans that are suited to the range of wetlands occurring in the landscape, as well as restoration strategies that are sensitive to geomorphic processes.

AUTHOR CONTRIBUTIONS

SG conceived and developed the classification system and wrote the paper. MG and WE contributed to the classification system and co-wrote the paper. NJ contributed toward the hillslope seeps section of the paper. DW critiqued the classification system and contributed to writing of the paper.

FUNDING

This research of SG was supported in part by the National Research Foundation of South Africa (Grant number: 118603).

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 05 December 2019
doi: 10.3389/fenvs.2019.00192

Food Web Structure and Trophic Dynamics of a Fish Community in an Ephemeral Floodplain Lake

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OPEN ACCESS

Edited by:
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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *04 September 2019*
Accepted: *21 November 2019*
Published: *05 December 2019*

Citation:
Peel RA, Hill JM, Taylor GC and Weyl OLF (2019) Food Web Structure and Trophic Dynamics of a Fish Community in an Ephemeral Floodplain Lake. Front. Environ. Sci. 7:192. doi: 10.3389/fenvs.2019.00192

In Africa, wetlands, such as shallow, ephemeral lakes provide ecosystem services, such as water purification, food supply, and flood control but are subject to dynamic flooding/drying cycles which vary in duration from years to decades. The stochastic nature of drying events subjects ephemeral lake fauna to persistent disturbance regimes, therefore understanding how biota respond to flooding and drying events is essential for their conservation and management. Primary production sources supporting consumer biomass in the shallow ephemeral Lake Liambezi (upper Zambezi Ecoregion), were investigated using stable isotope analysis, mixing models and stomach content analysis to investigate the following hypotheses: (1) algal primary production supports a higher consumer biomass than aquatic macrophytes; (2) the lake food chain is short, because the majority of fish fauna are detritivorous/herbivorous cichlids that are consumed by top predators; (3) fish community trophic structure will be similar between years; and (4) with short food chains and stochastic resource availability, there will be substantial competition for food among fish species. Results showed that phytoplankton production supported substantial consumer biomass in Lake Liambezi, with important contributions from macrophytes and associated detritus and/or periphyton. While particulate organic matter (POM) contributed substantially to the diet of herbivorous/detritivorous tilapiine cichlids (the backbone of Lake Liambezi's commercial fishery), considerable dietary carbon was likely also derived from aquatic plants and associated detritus and/or periphyton compared to other fishes. Three major food chains were identified in the lake. The phytoplankton-based pelagic food chain was longest, involving up to four trophic transfers. The benthic food chain based primarily on detritus of planktonic origin (but may also include macrophyte associated detritus/periphyton) was characterized by high levels of omnivory and involved up to three trophic transfers. The macrophytic detritus-based food chain was shortest, involving just two trophic transfers. Predators fed across all three food chains, but predominantly on the two benthic food chains. A combination of dietary overlap (amongst piscivores/predators, amongst insectivores), dietary specialization (tilapiine cichlids, alestids), the integration of multiple food chains and behavioral adaptation to changing dietary resources underpins the ability of Lake Liambezi's fish community to thrive under the stochastic nature of ephemeral lake ecosystems.

Keywords: floodplains, stable isotopes, food webs, lakes, fish communities

INTRODUCTION

Wetlands are diverse and productive systems (Ward et al., 1999, 2002) providing many economically valuable goods and services, such as water purification, food supply, and flood control (Baron et al., 2002). Among the most productive and important wetlands in Africa are large, shallow lakes (<5 m average depth, e.g., Lakes Chad and Chilwa) (Kalk et al., 1979; Carmouze et al., 1983), many of which occur in the drier tropics where surface water is scarce, making them extremely important both ecologically and economically (Kolding et al., 2016). With a high surface area relative to their volume, water replacement time in shallow lakes is generally short, making them especially sensitive to changes in water inputs (Talling, 2001). As a consequence, water level fluctuations are a dominant force controlling ecological processes in shallow lakes (Dumont, 1992; Wantzen et al., 2008; Kolding and van Zwieten, 2012). Many other environmental factors vary concurrently with fluctuations in water level (Talling, 1992), with important consequences for lake biota (Dumont, 1992; Talling, 2001).

Seasonal variation in the hydrological regime of tropical lakes becomes more pronounced with increasing latitude (Talling, 2001), and many endorheic lakes in the drier tropics experience large interannual fluctuations. In extreme cases, these are characterized by flooding and drying cycles, which can vary widely in duration from years to decades (e.g., Lake Chilwa; Kalk et al., 1979, and to some extent Lake Chad; Carmouze et al., 1983). Drying is a major disturbance in ephemeral lake ecosystems with severe consequences for populations of aquatic biota, but may be necessary for the maintenance of species diversity in ephemeral lakes as it increases habitat diversity, and promotes species coexistence by mediating biotic interactions (Dumont, 1992; Ward et al., 2002; Wantzen et al., 2008). The frequency and stochastic nature of drying events subjects ephemeral lake fauna to a persistent disturbance regime (Dumont, 1992) and thus understanding how biota respond to flooding and drying in ephemeral lakes is essential for their conservation and management.

Lake Liambezi is a shallow ephemeral floodplain lake situated in north-eastern Namibia. It is fed on an irregular basis by the Upper Zambezi and Kwando rivers, which overflow into the lake during years of extremely high flooding (Peel et al., 2015). The lake dried up in 1985 following 5 years of low floods in the inflowing rivers (Grobler and Ferreira, 1990). It remained largely dry until 2007, when it received a larger flood, followed by major flood in 2009, filling for the first time since the late 1970s. The lake reached a peak surface area of around 370 km^2 during successive floods in 2010 and 2011 and remained inundated, despite receiving minimal inflow until 2017. The lake hosts a thriving fish community (Peel et al., 2015, 2019) and consequently supports an active subsistence fishery, based primarily on large cichlid species, particularly *Oreochromis andersonii* and *Oreochromis macrochir*, however, the ephemeral nature of Lake Liambezi also puts it at risk of overfishing (Simasiku et al., 2017). The lake also supports extensive areas of aquatic macrophytes (Seaman et al., 1978; Peel et al., 2015), including vast, fragmented stands of the emergent reeds *Phragmites australis* (Gramineae) and *Typha capensis* (Typhaceae), which| provide shelter from wind and wave action, enabling the submerged macrophytes *Lagarosiphon ilicifolius* (Hydrocharitaceae) and *Najas horrida* (Hydrocharitaceae) to flourish in shallower areas. Seaman et al. (1978) hypothesized that these macrophytes acted as a "nutrient sponge," limiting the availability of nutrients to microalgae in the open lake, resulting in low algal growth potential. Seaman et al. (1978) and van der Waal (1985) thus considered macrophytes to be the most important primary producers supporting invertebrates and fishes in Lake Liambezi, a view widely held at the time (Howard-Williams and Junk, 1976; Soares et al., 1986; Bayley, 1989). Seaman et al. (1978) concluded that macrophytes must enter the food web mainly as detritus, and although there is some evidence that herbivores can remove an average of 40–48% of macrophyte biomass in aquatic ecosystems (Bakker et al., 2016), the direct consumption of macrophytes is rare among the Upper Zambezi ichthyofauna (van der Waal, 1985; Winemiller, 2004). Studies employing stable isotopes have since revealed that, despite being major primary producers in floodplain ecosystems, macrophytes, with some exceptions (e.g., Winemiller, 1996; Hoeinghaus et al., 2007; Zeug and Winemiller, 2008), generally contribute relatively little to aquatic food webs (Hamilton et al., 1992; Bunn and Boon, 1993; Forsberg et al., 1993; Thorp and Delong, 1994; Thorp et al., 1998; Lewis et al., 2001) and/or may have only very localized effects (Grosbois et al., 2017a). While these studies indicated that phytoplankton and periphyton, which usually constitute a small fraction of the potentially available carbon in floodplain ecosystems, are the principal carbon sources supporting invertebrates and fishes (Winemiller, 2004; Douglas et al., 2005).

This paper aims to investigate which primary production sources support consumer biomass in Lake Liambezi, a shallow ephemeral lake located in the upper Zambezi Ecoregion, to describe the trophic structure of the fish community and assess the trophic interactions among fish species, in order to discuss their potential influences in shaping its fish community. Using stable isotope analysis, mixing models and complimentary stomach contents analysis (fish only), this study set out to investigate the following hypotheses: (1) algal primary

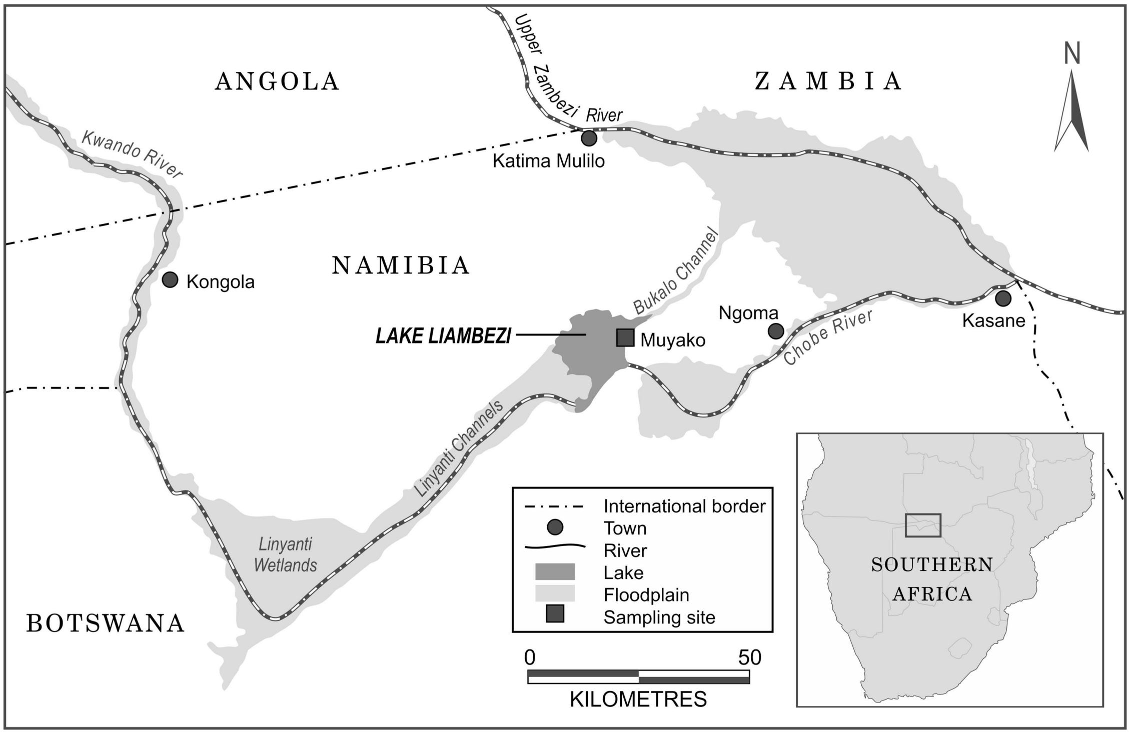

FIGURE 1 | Map of north-eastern Namibia illustrating the rivers and floodplains feeding into Lake Liambezi, and the location of the Lake Liambezi sampling site.

production (phytoplankton) supports a higher proportion of consumer biomass than aquatic macrophytes; (2) the lake food chain will be short, as a large component of the fish fauna comprises detritivorous and herbivorous fishes that may be consumed directly by top predators; (3) fish community trophic structure will be similar between years; and (4) with short food chains and the stochastic nature of resource availability in ephemeral systems, there will be substantial competition for food resources among fish species.

METHODS

Site Description

Lake Liambezi is a shallow ephemeral floodplain lake situated in the Zambezi Region of Namibia in southern Africa (**Figure 1**). With an average depth of ∼2.5 m, and a maximum depth of 7 m at its peak in 2010, the lake is relatively shallow (Peel et al., 2015) and annual temperatures range between 16.7 and 28.0°C, with a mean of 24.1°C (Seaman et al., 1978; Peel, 2016; Simasiku et al., 2017). Rains fall during austral summer from October to April, and are highly variable, averaging ∼700 mm in the north-east, declining gradually to 500 mm in the south-west (Mendelsohn and Roberts, 1997). The annual average evaporation rate is as high as 2,500 mm (Mendelsohn and Roberts, 1997). The composition of the Lake Liambezi fish community underwent a series of successional changes from its full inundation in 2007 until 2010, but remained largely the same from 2011 to 2014, suggesting the fish community may have reached maturity (Peel et al., 2019) and comprises 46 species from 10 families (**Supplementary Table 1**; Peel et al., 2015).

Stable Isotope Analysis

Stable isotope samples were collected during August 2011 and August 2012. Limited sampling of basal resources and fishes [*Oreochromis andersonii*, *Oreochromis macrochir*, *C. rendalli*, and *T. sparrmanii* (Cichlidae), $n = 11$ for each species] was additionally carried out in August 2014 to investigate dietary shifts in tilapiine cichlid species between years. Fishes and their potential food sources were collected across Lake Liambezi, including littoral areas, vegetated habitats and the open lake. Fish were sampled by D-netting (3 mm mesh), electrofishing, and using standardized multifilament gill nets (110 × 2.5 m, 11 panels) with stretched mesh sizes of 12, 16, 22, 28, 35, 45, 57, 73, 93, 118, and 150 mm and baited longlines (20 m long, 20 × 9/0 circle hooks on 80 lb monofilament snoods of 1 m in length). Nets were surface set between 18:00 and 19:00 and retrieved between 06:00 and 07:00 the following morning, in the eastern half of the lake, between the inflowing Bukalo Channel and Chobe River (**Figure 1**), in both open water and vegetated habitats. Fish were also purchased from local fishers. For most fishes, white muscle tissue was taken above the lateral line, for fish species <30 mm (e.g., *Micropanchax* spp, Poeciliidae family), whole bodies were used after removing the head, intestines and scales (skin however was not removed). Aquatic invertebrates were sampled using a scoop nets and by kick sampling, and whole bodies, and/or pooled individuals of the same species, were used for each sample. Zooplankton was collected using a Bongo net (500 µm mesh) towed on the water surface at night, sorted into the broadly defined groups of herbivorous or predatory zooplankton and then analyzed as bulk, pooled ($n = 10$) samples. Detritus was sampled using a cone dredge and aquatic macrophytes and filamentous algae were collected by hand. Particulate organic matter (POM) was collected by filtering between 1 and 2 L surface water, onto 0.45 μm pre-combusted (at 500°C for 4 h) glass fiber filters (Advantec).

All samples were oven dried at 50°C for 24–48 h, ground to a homogenous powder and then analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Europa Scientific 20-20 IRMS linked to an ANCA SL Prep Unit at IsoEnvironmental cc, South African Institute for Aquatic Biodiversity, Grahamstown, South Africa. Isotope values are expressed in delta notation according to:

$$\delta X = \left(R_{\text{sample}}/R_{\text{standard}} - 1\right) \times 1000,$$

where X is the element and R is the ratio of the heavy over the light isotope. The $\delta^{13}C$ and $\delta^{15}N$ values were reported as parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric nitrogen standards, respectively, and normalized to internal standards (casein and beet sugar), calibrated to the International Atomic Energy reference materials (IAEA-CH-3 and IAEA-CH-6 for $\delta^{13}C$, IAEA-N1 and IAEA-N2 for $\delta^{15}N$). Analytical precision was ± 0.07‰ for $\delta^{13}C$ and ± 0.12‰ for $\delta^{15}N$ for the 2011 samples and ± 0.08‰ for $\delta^{13}C$ and ± 0.12‰ for $\delta^{15}N$ for the 2012 samples.

Ethics approval was granted by the SAIAB Animal Ethics Committee (2013-07).

Food Web Structure

All fish samples were lipid corrected as described by Taylor et al. (2017a) and all isotope data collected in 2011 and 2012 were assessed separately, as baseline corrections for trophic positioning (e.g., Anderson and Cabana, 2007; Olsson et al., 2009) were not possible due to a lack of long-lived primary consumers living in the system. Aquatic insect and plant species were analyzed for $\delta^{13}C$ and $\delta^{15}N$ values and were then grouped into broad functional groups to ensure isotopically distinct resource assemblages for food-web interpretation and mixing model analyses (see below). Fishes were grouped according to a combination of taxonomic and feeding guilds as diets are often too flexible to be used solely for conclusive groupings (Yodzis and Winemiller, 1999; Jackson et al., 2001; Welcomme et al., 2006). The assessment of food web structure was based on a trophic enrichment of 1.5‰ for $\delta^{13}C$ (Sweeting et al., 2007a), and 3.2‰ for $\delta^{15}N$ (Sweeting et al., 2007b).

To investigate the proportional contribution of resources underpinning Lake Liambezi food webs separately for each year, Bayesian mixing models (MixSIAR; Stock and Semmens, 2016; Stock et al., 2018) were run using stable isotope data from all primary consumers (and some secondary consumers) (see **Table 1**) with $n \geq 10$ in both 2011 and 2012 (raw data), food sources (mean ± 1 SD) and discrimination factors of 1.5 ± 0.5‰ for $\delta^{13}C$ and 3.2 ± 0.5‰ for $\delta^{15}N$ as described above. The model was run with Markov chain Monte Carlo (MCMC) parameters of three chains of 300,000 iterations, a burn-in phase of 200,000 and a thinning of 100. Individuals as a random effect and both residual and process error were included in the model. The model generates posterior probability distributions that can be described by average estimates of the source contributions and their associated credible intervals. Convergence and diagnostic statistics were evaluated using the Gelman–Rubin test (all variables were $\leq$1.05). Note that while Bayesian mixing models can include some variability in predictions through the incorporation of error terms and informative priors (Parnell et al., 2010; Stock et al., 2018), there remains a mismatch in time integration between food resources and consumers, with the latter being typically more time integrated (Phillips et al., 2014). Thus, predicted proportional resource contributions to Lake Liambezi food webs will likely display some variation over time.

Because no long lived primary consumers were found in Lake Liambezi in order to baseline our datasets, variation in the isotope values ($\delta^{13}C$ and $\delta^{15}N$) of basal resources sampled in both years were assessed by multivariate statistical analyses performed using the PRIMER package, version 6 with PERMANOVA (Clarke and Gorley, 2006; Anderson et al., 2008). Analyses were performed on Euclidean distance measures of untransformed data. PERMANOVA were used to test for significant differences ($\alpha = 0.05$) between years and calculated using the Type III (partial) sums of squares with 9,999 unrestricted permutations and *post-hoc* pair-wise PERMANOVAs ($\alpha = 0.05$) were performed where appropriate. Important consumer species that showed large variation in $\delta^{13}C$ between 2011 and 2012 were also tested for significant differences ($\alpha = 0.05$) using univariate PERMANOVAs as described above. Here, the additional data collected in 2014 were used to determine whether the differences in $\delta^{13}C$ values of the tilapiine cichlids between years represented a permanent dietary shift, or simply inter-annual dietary variation.

Community Metrics

The trophic structure of the fish community was then compared between 2011 and 2012 using six quantitative isotope metrics (Layman et al., 2007; Jackson et al., 2011); nitrogen range (NR); carbon range (CR); mean distance to centroid (CD), providing a measure of trophic diversity; mean nearest neighbor distance (MNND), which estimates the density and clustering of species within the community; standard deviation of the nearest neighbor distance (SDNND), which gives a measure of the evenness of species packing in isotopic biplot space; and the sample size corrected standard ellipse area (SEA_c), which provides a bivariate measure of the mean core isotopic niche of a community. The degree of SEA_c overlap between communities was calculated to give a quantitative measure of dietary similarity (Jackson et al., 2012). Only fish species collected in both years with a sample size $\geq$3 were included in the analyses. All metrics were calculated using the Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al., 2011) package in the R statistical computing programme (R Core Team, 2013), and bootstrapped ($n = 10{,}000$) to allow comparisons of 2011 and 2012 datasets that differed in sample size.

Trophic Structure and Species Interactions

The trophic structure of the fish community sampled in 2011 only was further resolved by calculating the SEA_c of each

TABLE 1 | Carbon and nitrogen stable isotope values (mean ± standard deviation) of fish species, invertebrate groups and basal carbon sources sampled in Lake Liambezi in 2011 and 2012, and the taxonomic/feeding group to which species were assigned for broad food web analysis.

Species	*Family*	2011			2012			Group
		N	δ^{13}C	δ^{15}N	*N*	δ^{13}C	δ^{15}N	
FISH								
Brycinus lateralis	Alestidae	28*	−26.71 ± 1.40	9.82 ± 0.85	32*	−27.89 ± 2.20	9.81 ± 0.98	Alestids
Rhabdalestes maunensis	Alestidae	21*	−27.97 ± 0.93	9.89 ± 0.41	10*	−26.15 ± 1.31	9.64 ± 0.62	Alestids
Enteromius barnardi	Cyprinidae	1	−29.16	8.71	–	–	–	Cyprinids
Enteromius bifrenatus	Cyprinidae	3	−21.66 ± 1.19	7.36 ± 0.37	7	−31.31 ± 0.99	9.11 ± 0.88	Cyprinids
Enteromius haasianus	Cyprinidae	6	−24.45 ± 0.84	8.26 ± 0.39	–	–	–	Cyprinids
Enteromius poechii	Cyprinidae	8	−23.14 ± 2.96	8.25 ± 0.81	2	−27.10 ± 0.70	8.36 ± 0.03	Cyprinids
Enteromius radiatus	Cyprinidae	21*	−25.55 ± 2.01	8.38 ± 0.56	11*	−26.32 ± 0.46	8.50 ± 0.89	Cyprinids
Enteromius unitaeniatus	Cyprinidae	9	−27.07 ± 0.80	9.04 ± 0.36	–	–	–	Cyprinids
Coptostomobarbus wittei	Cyprinidae	3	−26.85 ± 2.21	9.90 ± 0.55	–	–	–	Cyprinids
Labeo cylindricus	Cyprinidae	1	−24.27	7.78	1	−24.54	8.03	Cyprinids
Pharyngochromis acuticeps	Cichlidae	21*	−26.94 ± 2.02	8.46 ± 0.76	16*	−27.60 ± 2.28	8.92 ± 1.17	Benthic cichlids
Pseudocrenilabrus philander	Cichlidae	17*	−24.00 ± 2.41	9.42 ± 0.73	5	−23.89 ± 1.05	8.54 ± 0.79	Benthic cichlids
Sargochromis codringtonii	Cichlidae	20*	−24.68 ± 2.12	8.30 ± 0.69	1	−23.93	8.82	Benthic cichlids
Sargochromis carlottae	Cichlidae	–	–	–	3	−25.37 ± 2.62	9.47 ± 1.66	Benthic cichlids
Schilbe intermedius	Schilbeidae	25	−25.26 ± 2.24	8.95 ± 1.04	29	−26.08 ± 1.82	9.50 ± 0.83	Generalist predators
Clarias ngamensis	Clariidae	11	−24.46 ± 2.20	8.92 ± 0.46	1	−24.23	9.8	Generalist predators
Clarias theodorae	Clariidae	1	−22.93	10.55	–	–	–	Generalist predators
Synodontis spp.	Mochokidae	17	−27.84 ± 2.01	9.25 ± 0.88	3	−26.81 ± 0.36	10.30 ± 0.51	Generalist predators
Marcusenius altisambesi	Mormyridae	13*	−25.67 ± 2.27	7.51 ± 0.76	2	−27.74 ± 3.52	7.70 ± 0.21	Mormyrids
Petrocephalus cf. *okavangensis*	Mormyridae	7	−26.08 ± 1.01	9.11 ± 0.55	6	−25.59 ± 1.74	8.93 ± 0.40	Mormyrids
Mormyrus lacerda	Mormyridae	1	−30.63	9.3	–	–	–	Mormyrids
Cyphomyrus cubangoensis	Mormyridae	–	–	–	1	−26	9.2	Mormyrids
Serranochromis macrocephalus	Cichlidae	16	−25.49 ± 2.21	10.35 ± 0.78	10	−25.56 ± 2.12	10.48 ± 1.33	Piscivores
Serranochromis robustus jallae	Cichlidae	3	−20.57 ± 0.65	9.37 ± 0.41	1	−21.59	9.37	Piscivores
Hepsetus cuvieri	Hepsetidae	11	−23.69 ± 1.99	9.91 ± 0.80	10	−24.61 ± 3.19	10.36 ± 1.32	Piscivores
Clarias gariepinus	Clariidae	5	−24.74 ± 2.36	9.88 ± 0.46	7	24.33 ± 1.62	10.04 ± 0.73	Piscivores
Oreochromis andersonii	Cichlidae	10*	−26.14 ± 4.09	6.34 ± 0.88	20*	−27.90 ± 1.97	7.73 ± 1.41	Tilapiine cichlids
Oreochromis macrochir	Cichlidae	12*	−22.46 ± 1.89	5.38 ± 0.68	14*	−24.49 ± 2.76	5.15 ± 0.90	Tilapiine cichlids
Coptodon rendalli	Cichlidae	18*	−21.92 ± 3.86	7.12 ± 0.98	10*	−25.75 ± 2.47	6.70 ± 1.14	Tilapiine cichlids
Tilapia sparrmanii	Cichlidae	16*	−24.55 ± 1.78	7.60 ± 1.38	18*	−26.95 ± 3.44	7.54 ± 1.35	Tilapiine cichlids
Tilapia ruweti	Cichlidae	2	−21.74 ± 1.08	8.18 ± 1.17	–	–	–	Tilapiine cichlids
Micropanchax johnstoni	Poeciliidae	11*	−26.20 ± 2.11	9.78 ± 0.50	6	−23.92 ± 1.00	8.34 ± 0.53	Topminnows
Micropanchax hutereaui	Poeciliidae	–	–	–	4	−22.06 ± 0.72	8.31 ± 0.38	Topminnows
INVERTEBRATES								
Aquatic insects	–	10	−28.32 ± 3.62	6.14 ± 2.79	24	−26.67 ± 2.40	5.95 ± 1.30	–
Decapods	–	10	−23.96 ± 0.94	7.22 ± 0.63	5	−25.43 ± 0.62	5.79 ± 0.21	–
Herbivorous zooplankton	–	3	−30.75 ± 0.97	6.08 ± 0.81	–	–	–	–
Predatory zooplankton	–	9	−30.16 ± 1.35	10.05 ± 0.68	2	−29.66 ± 0.08	9.89 ± 0.03	–
BASAL RESOURCES								
POM	–	17	−30.71 ± 1.63	4.02 ± 0.54	16	−29.62 ± 1.42	4.16 ± 0.87	–
Detritus	–	30	−17.68 ± 4.09	3.25 ± 1.14	–	–	–	–
Emergent plants**	–	–	–	–	15	−25.72 ± 1.28	2.46 ± 2.92	–
Submerged plants[†]	–	7	−21.47 ± 5.76	3.00 ± 2.82	25	−19.54 ± 3.62	0.93 ± 1.82	–
Filamentous algae[‡]	–	–	–	–	6	−23.20 ± 1.52	1.63 ± 0.43	–

*Indicate which fish species were included in the Bayesian mixing models (MixSIAR).

**Emergent plants included Phragmites australis, Typha capensis, Nymphaea nouchali, Vossia cuspidate, and Ludwigia sp.

[†] Submerged plants included Potamogeton thunbergii, Potamogeton tiroides, Potamogeton schweinfurthii, Ceratophyllum demersum, Najas horrida, Lagarosiphon ilicifolius and Utricalaria sp.

[‡] Filamentous algae included Spirogyra sp. and Cladophora glomerta.

taxonomic/feeding group, and the % of SEA_c overlap between groups (as fishes were more comprehensively sampled in 2011). The SEA_c and % overlap of individual species within important consumer groups were then calculated to elucidate interspecific trophic interactions and explore potential competition in the lacustrine fish community. The groups of species examined included the alestids, which have been a dominant component of the fish fauna in the lake since it filled, the tilapiine cichlids on which the fishery is based, generalist predators that include the highly abundant *Schilbe intermedius* (Schilbeidae), and piscivores which may influence community food web structure (van der Waal, 1985; Peel et al., 2015).

Stomach Content Analysis

To aid in interpreting the results of the stable isotope analyses, stomach contents were conducted the four most abundant, large piscivorous fish species in Lake Liambezi; *S. intermedius, Clarias gariepinus* (Clariidae), *Hepsetus cuvieri* (Hepsetidae), and *Serranochromis macrocephalus* (Cichlidae), which likely influenced food web structure *via* predation, and one small zooplanktivorous species, *Brycinus lateralis* (Alestidae), which was a major component of the Lake Liambezi fish fauna (Peel et al., 2015). Fish were sampled using standardized multifilament and baited longlines (see above). All fish caught were identified to species level according to Skelton (2001, 2016), measured to the nearest mm and weighed to the nearest gram. Samples of the piscivorous species were collected on five occasions between October 2013 and December 2014, and their stomach contents were examined in the field. *Brycinus lateralis* were sampled in February 2013, and preserved whole in the field in 10% buffered formalin. Stomach contents of *B. lateralis* were later examined under a dissecting microscope in the laboratory, identified to the lowest practical taxonomic level, counted and weighed to the nearest 0.1 gram after blotting dry. For *B. lateralis*, an indirect volumetric assessment of each food category was used (Booth and McKinlay, 2001), because food items could not be weighed with sufficient precision.

Dietary composition of the five study species was assessed by calculating the index of relative importance (IRI; Pinkas et al., 1971) of each prey item, as:

$$IRI = (\%N + \%W) \times \%FO,$$

where $\%N$ and $\%W$ are the number and weight of each prey item as a percentage of all prey, and $\%FO$ is the number of stomachs containing a specific prey item as a percentage of all sampled stomachs. For *B. lateralis* $\%V$, the volume of each prey item as a percentage of all prey, was used in place of $\%W$. The IRI for each prey item was then expressed as a percentage of the sum of IRI values for all prey items (%IRI).

RESULTS

Stable Isotope Analysis

Food Web Structure

In 2011, 424 samples were collected for stable isotope analysis, comprised of three basal carbon sources, four general invertebrate groups and 30 fish species (**Table 1**). In 2012, 318 samples were collected, comprising four basal carbon sources, three general invertebrate groups and 26 fish species. The $\delta^{13}C$ values of basal resources ranged between −33 and −9‰ in 2011, and between −32 and −13‰ in 2012 (**Table 1**; **Figure 2**). POM had the lowest $\delta^{13}C$ of all basal resources, averaging approximately −30‰ in both years. The $\delta^{13}C$ of emergent plants and filamentous algae, both of which were only collected in 2012, averaged −26 and −23‰, respectively. Submerged plants had average $\delta^{13}C$ values of −21 and −20‰ in 2011 and 2012, respectively. Detritus, which was only collected in 2011, was the most enriched with a $\delta^{13}C$ value of −18‰ but was not isotopically distinct from submerged plant samples, suggesting a substantial proportion of the detritus was of submerged plant origin. The $\delta^{15}N$ values of different basal resources sampled in 2011 were similar (∼3–4‰), but in 2012, plants and filamentous algae had much lower $\delta^{15}N$ values than POM. The isotope values of submerged plants (PERMANOVA; *Pseudo-F* $= 2.04$, $P = 0.145$) and POM (PERMANOVA; *Pseudo-F* $= 3.51$, $P = 0.053$) did not differ significantly between years. Note that although periphyton has been identified as one of the principal carbon sources supporting fish and invertebrate communities in floodplain ecosystems (Winemiller, 2004; Douglas et al., 2005), periphyton isotope data was not available for this study. However, as the isotopic values of macrophytes and associated periphyton (e.g., Neill and Cornwell, 1992; de Kluijver et al., 2015; Pettit et al., 2016) are often indistinguishable, for the purposes of interpretation, macrophytes and periphyton are considered together.

Overall, mixing model results for primary and secondary fish consumers showed that 58% of modeled fish species in 2011 and 87.5% in 2012 had substantial dietary POM contributions of >15%. In 2011 83% of fish species also had strong dietary contributions (>12.5%) of submerged plants. Briefly; topminnows and alestids relied almost exclusively on zooplankton and aquatic invertebrates in both years, *Coptodon rendalli* relied primarily on detritus and submerged plants in 2011 and decapods, POM and filamentous algae in 2012; mormyrids (data only available for 2011) were strongly opportunistic, feeding on a variety of sources including, aquatic invertebrates, zooplankton, POM, and submerged plants; tilapiine cichlids depended on submerged plants, POM and in some case zooplankton and aquatic invertebrates in 2011, vs. POM, zooplankton and filamentous algae in 2012; and benthic cichlids preferred POM, zooplankton in both years, as well as submerged plants and detritus in 2011 (**Figures 3**, **4**, **Supplementary Table 2**). The low contribution values of any food source to *Tilapia sparrmanii* diet in 2012 suggests some basal resources may have been missed.

Both 2011 and 2012 data suggest that POM was the ultimate driver of the Lake Liambezi food web (either directly or indirectly), with three potential energy pathways by which basal resources were assimilated into the food web. Firstly, in 2011, the isotopic position of herbivorous zooplankton indicated that their diets likely consisted exclusively of POM. Secondly, aquatic invertebrates (including decapods in 2012) were similarly positioned, but demonstrated more variable $\delta^{13}C$

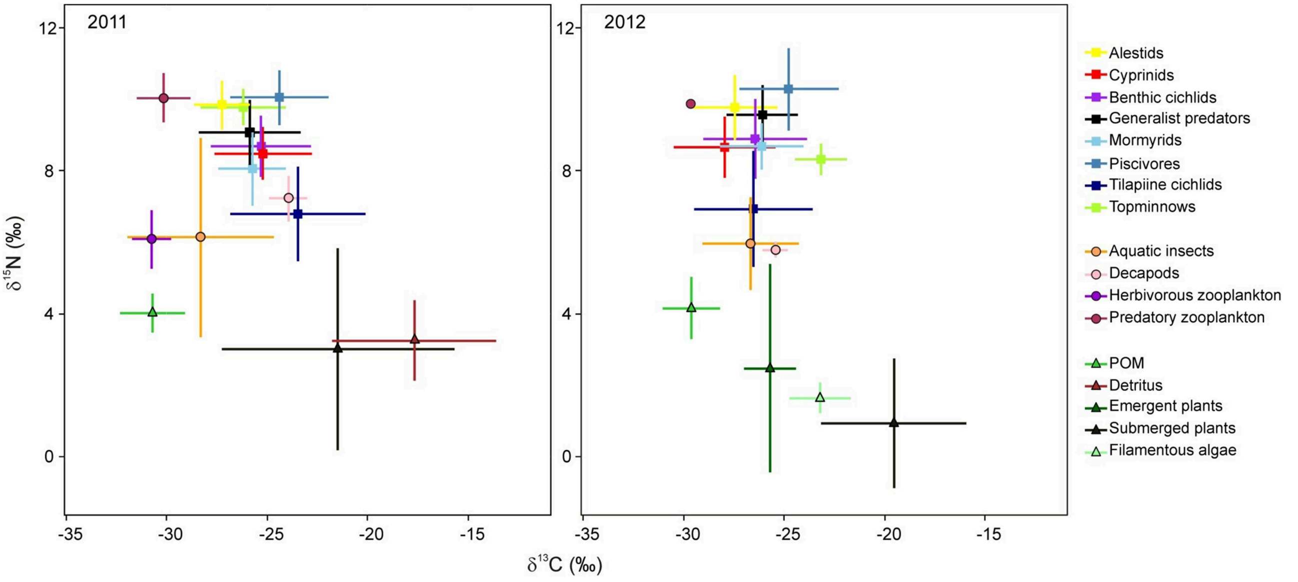

FIGURE 2 | Stable δ^{13}C-δ^{15}N isotopic bi-plots of fish groups and their potential food sources from Lake Liambezi in 2011 and 2012. Data points represent the mean ± standard deviation for each group.

values, indicating that while this diverse group relies primarily on POM, they likely also assimilate carbon from a range of other basal resources, including emergent plants and potentially their associated detritus and/or periphyton. The aquatic invertebrate group consisted mainly of benthic organisms, so their main source of POM likely settled out of the water column, possibly in the form of planktonic detritus (e.g., sinking phytoplankton). Thirdly, the relatively depleted values of δ^{15}N and slightly enriched δ^{13}C values (in 2012 only) of tilapiine cichlids relative to other fish species, suggest that although POM was a substantial contributor to tilapiine cichlid diet, considerable amounts of their dietary carbon were also derived from aquatic plants and detritus/periphyton compared to other consumers (**Figure 2**). However, as only *Coptodon rendalli* feed directly on macrophytes, this carbon was likely incorporated as detritus. As degradation does not often effect isotopic change in macrophytes (Macko and Estep, 1984; Currin et al., 1995; Fellerhoff et al., 2003; Hill and McQuaid, 2009), it is likely the sampled detritus was of submerged plant origin. All three of these primary consumers (herbivorous zooplankton; aquatic invertebrates/decapods and tilapiine cichlids) were regular dietary components for other fish species (**Table 2**).

The average δ^{13}C of tilapiine cichlids showed a 3‰ depletion in 2012, possibly indicating a shift to a more POM based diet. Further sampling of the tilapiine cichlids was carried out in 2014 to establish whether the shift to a lower δ^{13}C diet was permanent. δ^{13}C values did not differ significantly between years for *O. andersonii* (PERMANOVA; *Pseudo-F* = 1.53, *P* = 0.233) or *O. macrochir* (PERMANOVA; *Pseudo-F* = 2.33, *P* = 0.113). However, δ^{13}C values differed significantly between years for *C. rendalli* (PERMANOVA; *Pseudo-F* = 8.48, *P* = 0.001) and *T. sparrmanii* (PERMANOVA; *Pseudo-F* = 4.69, *P* = 0.015), with δ^{13}C significantly lower in 2012 compared to 2011 and 2014. Two other groups of fishes showed changes in trophic position between years; cyprinids showed a depletion in δ^{13}C, and topminnows an enrichment in δ^{13}C coupled with decrease in δ^{15}N between 2011 and 2012, however as minor components of the fish community, they were unlikely to alter major pathways of energy flow through the food web and were thus not investigated further. Community-wide stable isotope metrics were subsequently used to quantitatively assess the similarity of fish communities between years.

Community Metrics

The NR and CR of the fish community in 2012 were higher than in 2011, suggesting that both the trophic length and range of basal resources used by the fish community in 2012 was greater. However, the average degree of trophic diversity (CD), was similar between years. Lower MNND and SDNND in 2011 indicate greater density and evenness of species packing in bi-plot space (**Table 3**). For each metric, the difference between years was relatively small, and the overlap of 95% confidence intervals was substantial. The core isotopic niche area (SEA$_c$) of the whole fish community (**Figure 5A**) was slightly larger in 2012 compared to 2011, corroborating results of the other metrics. The degree of overlap between years was also significant; the 2011 fish community SEA$_c$ overlapped with the 2012 fish community SEA$_c$ by 68.3%, whereas the 2012 SEA$_c$ overlapped with the 2011 SEA$_c$ by an even greater 76.8%. Overall, the tropic structure of the fish communities sampled in 2011 and 2012 were thus very similar, however, the inter-annual variations in trophic positions of the tilapiine cichlids, cyprinids and topminnows precluded the combination of both datasets. As a result, further analyses on the fish community interactions were based only on the more comprehensive 2011 dataset.

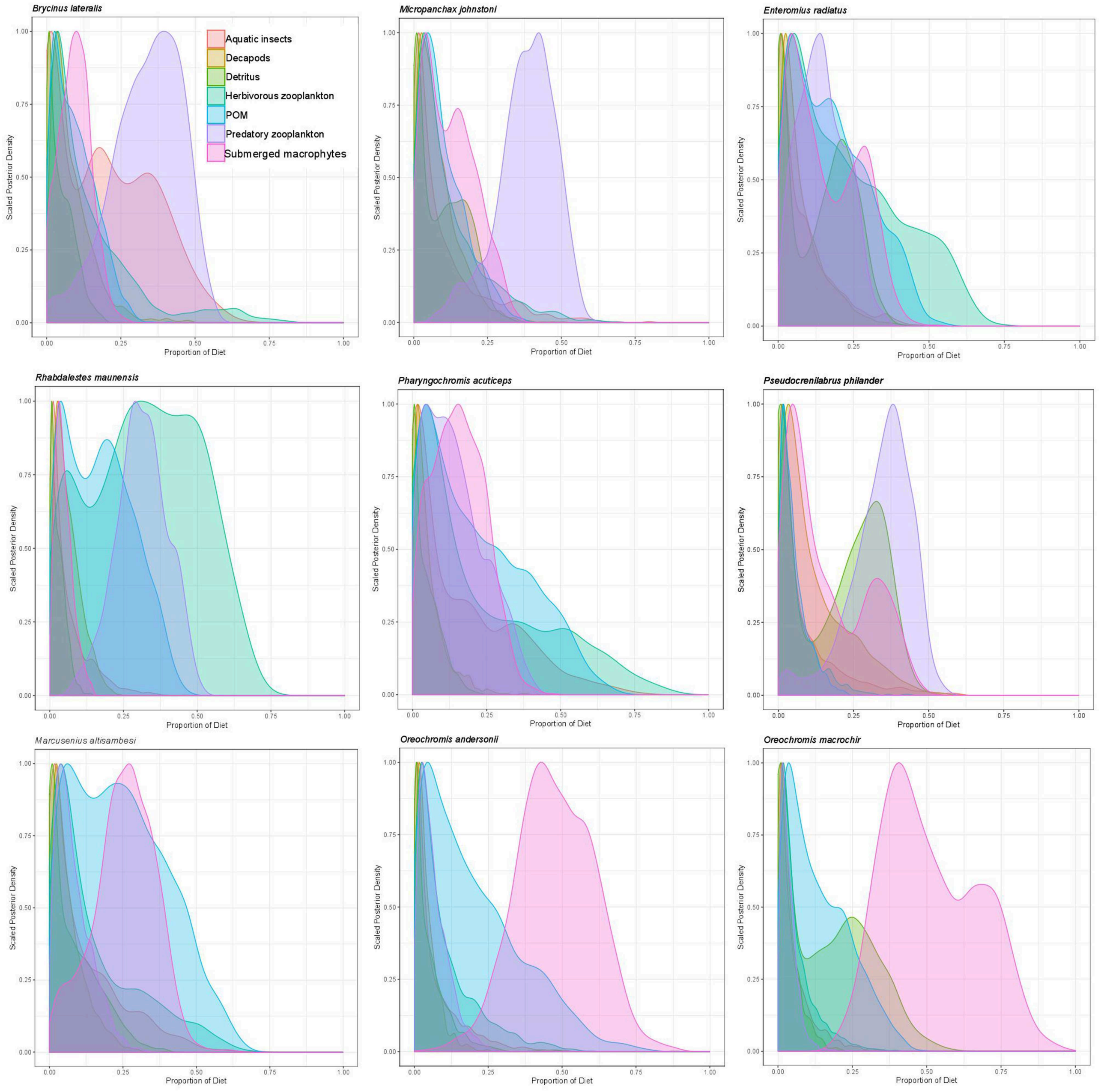

FIGURE 3 | Proportional resource contributions to primary and secondary fish consumers as determined by Bayesian MixSIAR mixing models for 2011.

Trophic Structure and Species Interactions

Tilapiine cichlids, despite being the backbone of the Lake Liambezi gill net fishery, made up only 4% of the CPUE (kg net^{-1} night^{-1}) (**Supplementary Table 1**). They occupied the lowest trophic position in the overall fish community and did not show much SEA$_c$ overlap with other groups, indicating that they are the only primary consumers in the fish community. Their SEA$_c$ was large, suggesting higher trophic diversity compared to other groups. At the next trophic level there was considerable overlap in isotopic space between cyprinids, benthic cichlids, mormyrids and generalist predators, all of which had similar sized SEA$_c$. These four groups were most likely primarily dependent upon aquatic invertebrates for their food. Alestids and topminnows occupied a slightly higher trophic level, with considerable SEA$_c$ overlap between the two groups. Alestids had the smallest SEA$_c$ of any group, indicative of dietary specialization. Their elevated trophic position and relatively low δ^{13}C reflects a diet composed of both herbivorous and predatory zooplankton. Piscivores occupied the highest trophic level in Lake Liambezi and overlapped relatively little with other groups (**Figure 5B**;

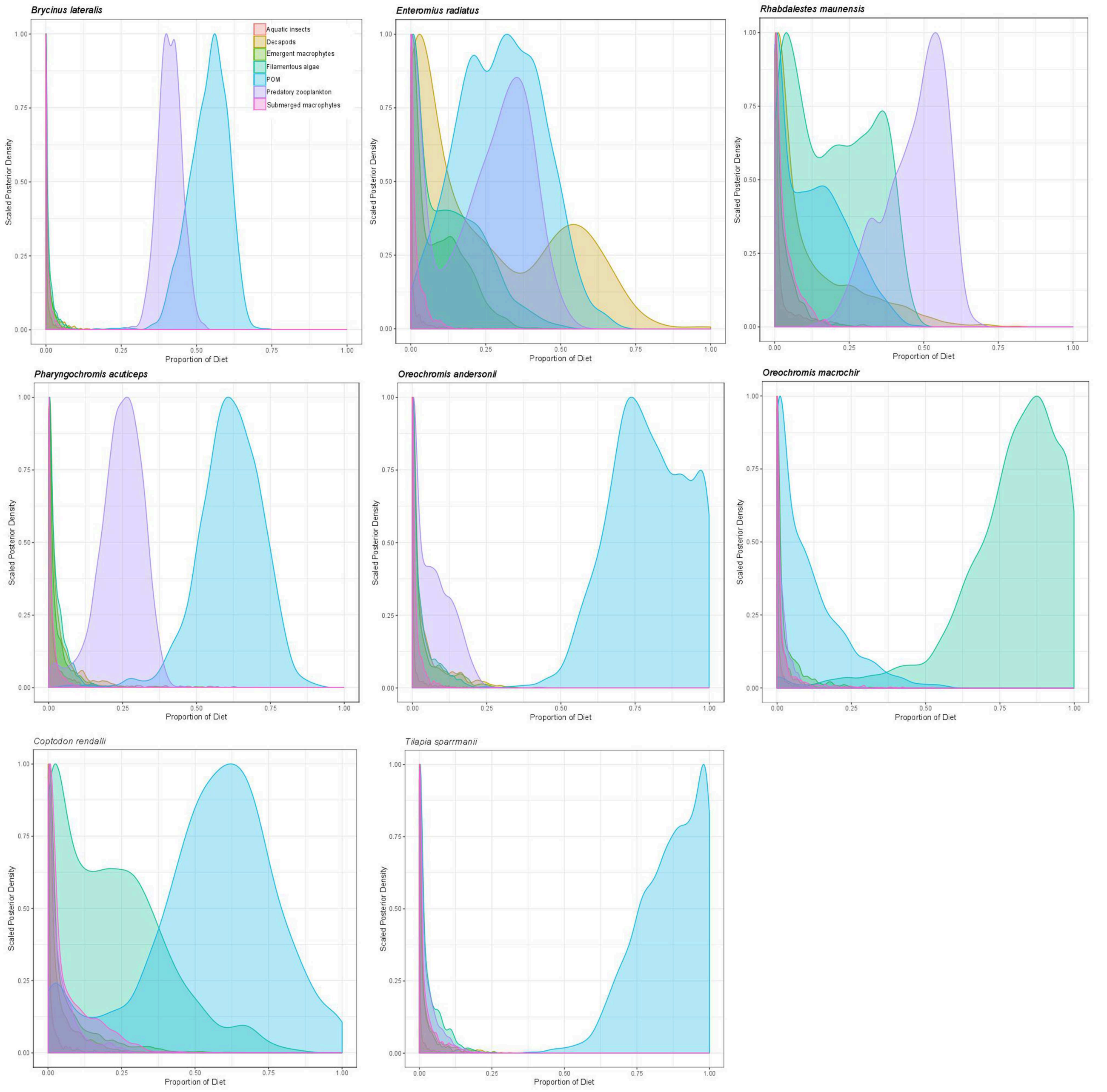

FIGURE 4 | Proportional resource contributions to primary and secondary fish consumers as determined by Bayesian MixSIAR mixing models for 2012.

Table 4). The trophic positions of individual fish species within important consumer groups were examined further to elucidate interspecific trophic interactions.

The trophic level of the alestids *B. lateralis* and *Rhabdalestes maunensis* was similar to that of the piscivores in Lake Liambezi. *Brycinus lateralis*, the larger of the two alestids, had a SEAc of 3.36‰^{2}. *Rhabdalestes maunensis* had a significantly smaller SEAc of 1.24‰^{2}, 48.9% of which was overlapped by *B. lateralis.* In contrast, only 18.1% of the core niche of *B. lateralis* was overlapped by *R. maunensis* (**Figure 5C**).

Of the four tilapiine cichlids, *O. macrochir* had the smallest SEAc and lowest trophic position, indicating this species was a highly specialized primary consumer (**Figure 5D**). The much larger isotopic niche of *O. andersonii* overlapped with that of *O. macrochir* by approximately one third (**Table 5**). *Oreochromis andersonii* generally had a lower δ^{13}C and higher δ^{15}N than *O. macrochir*. *Coptodon rendalli* had the largest SEAc of the four species, perhaps reflective of the extremely variable isotope values of submerged plants. *Coptodon rendalli* occupied a higher trophic level than both *Oreochromis* spp. and did not overlap

TABLE 2 | Stomach contents of fish species (no. of stomachs; % empty) and their length, by % number (*%N*), % weight (*%W*) and % frequency of occurrence (*%FO*), and the % index of relative importance (*%IRI*) of each prey category.

Species and prey category	**TL/FL (mm)**	***n***	**ID**	***%N***	***%W***	***%FO***	***%IRI***
Clarias gariepinus (63 stomachs; 75% empty)	434–1,220 TL	16					
Fish			Fish remains	23.53	8.27	6.35	5.50
			Cichlidae	76.47	91.73	20.63	94.50
Hepsetus cuvieri (125 stomachs; 72% empty)	195–386 TL	35					
Fish			Fish remains	26.32	8.22	8.00	7.91
			Cichlidae	71.05	89.66	20.00	91.98
			Alestidae	2.63	2.12	0.80	0.11
Serranochromis macrocephalus (72 stomachs; 81% empty)	120–302 TL	14					
Fish			Fish remains	35.29	30.00	8.11	40.48
			Cichlidae	17.65	13.79	4.05	9.75
			Alestidae	41.18	53.45	6.76	48.88
Aquatic invertebrates			Insect remains	5.88	2.76	1.35	0.89
Schilbe intermedius (241 stomachs; 43% empty)	90–273 FL	137					
Fish			Fish remains	9.73	10.45	15.35	12.54
			Cichlidae	13.57	69.36	19.09	64.08
			Alestidae	1.36	10.83	2.07	1.02
			Cyprinodontidae	0.45	0.24	0.41	0.01
Aquatic invertebrates			Insect remains	8.60	1.89	15.77	6.69
			Ephemeroptera	36.20	4.83	7.47	12.41
			Trichoptera	0.23	0.03	0.41	0.00
			Coleoptera	0.23	0.00	0.41	0.00
			Hemiptera	0.23	0.00	0.41	0.00
			Odonata	0.90	0.24	1.66	0.08
			Diptera	19.68	0.86	3.32	2.76
			Decapoda	1.13	0.37	1.24	0.08
			Gastropoda	0.23	0.02	0.41	0.00
Terrestrial invertebrates			Lepidoptera	0.23	0.07	0.41	0.00
			Orthoptera	0.90	0.29	1.66	0.08
			Araneae	0.23	0.03	0.41	0.00
			Insect eggs	5.66	0.17	0.83	0.20
			Detritus	0.45	0.31	0.83	0.03
Brycinus lateralis (29 stomachs; 23% empty)	24–127 FL	30			*%V*		
Fish			Fish remains	4.19	20.05	20.51	7.88
Aquatic invertebrates			Insect remains	9.95	27.11	46.15	27.09
			Ephemeroptera	2.62	4.33	7.69	0.85
			Trichoptera	2.09	4.10	7.69	0.75
			Odonata	0.52	1.67	2.56	0.09
			Diptera	53.93	18.73	41.03	47.22
			Zooplankton	18.85	0.75	25.64	7.96
			Insect eggs	4.71	12.99	23.08	6.47
			Plant matter	1.05	4.93	5.13	0.49

Note for Brycinus lateralis, % volume (%V) replaces %W.

with either. It did, however, overlap with *T. sparrmanii* which had a slightly smaller and more laterally compressed SEAc, suggesting a narrower range of basal resources, but large variation in trophic level.

The core niche areas of piscivores and generalist predators were examined together (**Figure 5E**), with the two most abundant generalist predators, *S. intermedius* and *Clarias ngamensis* occupying a lower trophic level than the top piscivores. *Schilbe intermedius* had the larger SEAc of the two species, which overlapped considerably with that of *C. ngamensis* (**Table 5**). There was also extensive SEAc overlap among the three piscivores. Half the SEAc of *H. cuvieri*, and two thirds the SEAc of *C. gariepinus* were overlapped by *S. macrocephalus*. *Serranochromis macrocephalus* had a similarly large SEAc size to that of *S. intermedius*. The large isotopic niche of *S. macrocephalus* revealed by stable isotope analysis is contrary to the dietary specialization inferred from stomach contents analysis. However, the smaller SEAc of *H. cuvieri* and *C. gariepinus* appear to confirm that they are relatively specialized piscivores. For both *H. cuvieri* and *C. gariepinus*, $\delta^{15}N$ tended to decrease with increasing $\delta^{13}C$.

TABLE 3 | Stable isotope community metrics (mean with 95% CI in parentheses) comparing the trophic structure of fish communities sampled from Lake Liambezi in 2011 and 2012.

Metric	2011	2012
NR	5.03 (4.43–5.66)	5.67 (4.84–6.74)
CR	6.95 (5.59–8.89)	7.95 (6.72–9.49)
CD	2.12 (1.88–2.38)	2.05 (1.83–2.28)
MNND	0.87 (0.67–1.08)	0.98 (0.80–1.18)
SDNND	0.54 (0.33–0.79)	0.79 (0.53–1.06)
SEA_C	11.93 (10.07–14.15)	13.42 (11.89–15.23)
Sample size (*n*)	259	212

NR, $\delta^{15}N$ range; CR, $\delta^{13}C$ range; CD, mean distance to centroid; MNND, mean nearest neighbor distance; SDNND, standard deviation of nearest neighbor distance; SEA_C, core isotopic niche area of the community (‰^{2}).

Stomach Contents Analysis

Clarias gariepinus and *H. cuvieri* gut contents comprised exclusively fish, while *S. macrocephalus* also preyed on aquatic invertebrates (**Table 2**). Cichlidae were the only fish identified in the stomachs of *C. gariepinus*. In addition to cichlids, alestids were among the prey of *H. cuvieri* and *S. macrocephalus*. Cichlidae constituted the bulk of *H. cuvieri* prey, while alestids were more important to *S. macrocephalus*. The most frequently identified cichlid prey species were *Tilapia sparrmanii* and *Pharyngochromis acuticeps* but *Oreochromis* spp. also contributed substantially to the diet of *C. gariepinus*.

A diverse range of prey were recorded from full stomachs of *S. intermedius*, including fish, aquatic and terrestrial invertebrates, insect eggs, and detritus (**Table 2**). Fish, cichlids in particular, were the most important food source for *S. intermedius* in Lake Liambezi, with the most commonly identified cichlid species being *T. sparrmanii* and *P. acuticeps*. Ephemeroptera were the only insect order to contribute substantially to the diet of *S. intermedius*.

Identifiable items in full stomachs of *B. lateralis* included fish, aquatic invertebrates, insect eggs and plant matter (**Table 2**). A large portion of the aquatic invertebrate prey were masticated and could not be identified further. Dipteran larvae, primarily *Chaobrus* spp., were the most important prey item identified, accounting for nearly half of the diet of *B. lateralis*. Planktonic

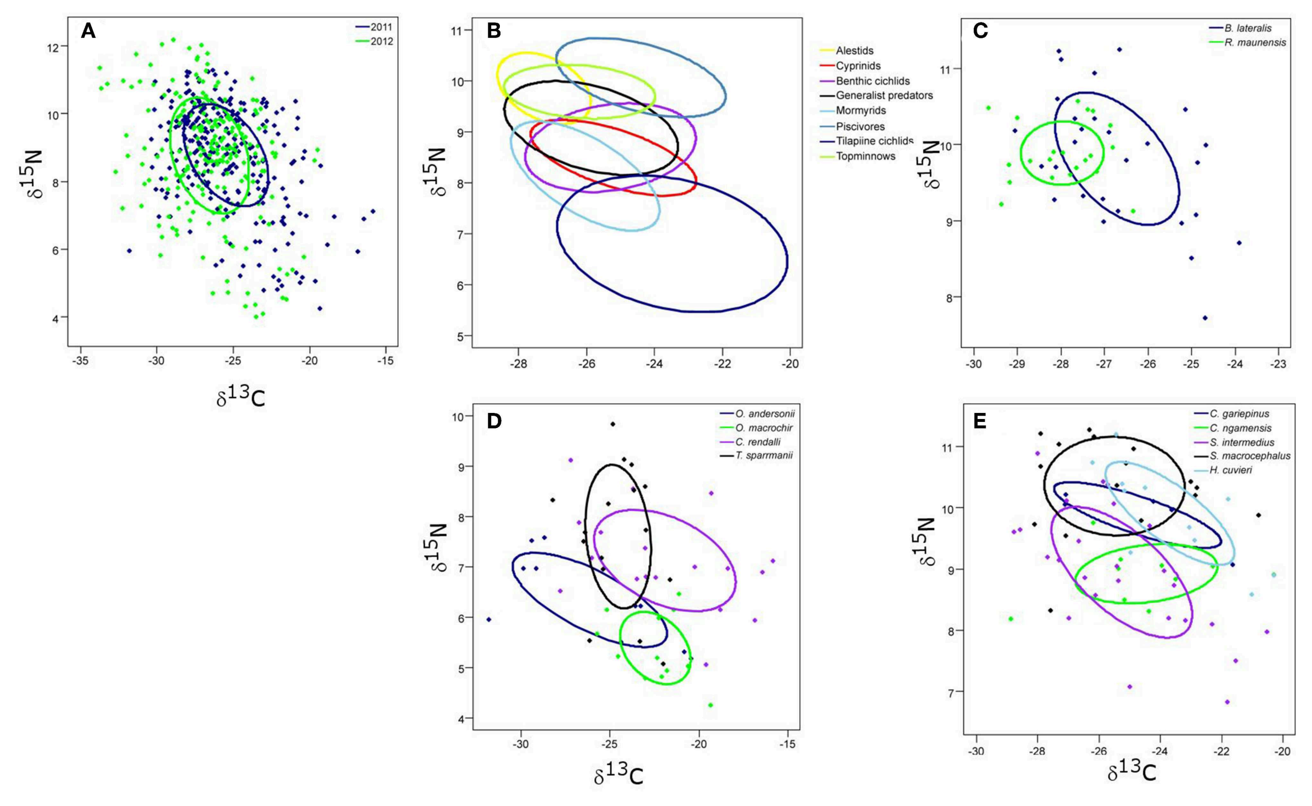

FIGURE 5 | The core isotopic niche areas (SEAc) of **(A)** 2011 and 2012 complete fish communities; **(B)** all fish groups; **(C)** alestid species; **(D)** the four tilapiine cichlid species; and **(E)** the predatory fish species in Lake Liambezi in 2011.

TABLE 4 | The core isotopic niche area (SEAc) and percent overlap between fish groups in Lake Liambezi in 2011.

	SEAc	Alestids	Cyprinids	Benthic cichlids	Generalist predators	Mormyrids	Piscivores	Tilapiine cichlids	Topminnows
Alestids	2.80		1.2	2.3	23.1	0.0	3.2	0.0	53.8
Cyprinids	4.47	1.9		55.1	45.5	41.9	0.0	5.6	0.0
Benthic cichlids	6.69	5.6	82.5		66.4	54.7	4.7	2.8	13.0
Generalist predators	6.78	56.0	69.0	67.2		34.1	8.2	0.0	55.7
Mormyrids	5.71	0.1	53.6	46.7	28.8		0.0	15.7	0.0
Piscivores	5.31	6.0	0.0	3.7	6.4	0.0		0.0	40.2
Tilapiine cichlids	13.77	0.0	17.3	5.9	0.0	37.8	0.0		0.0
Topminnows	3.64	70.0	0.0	7.1	29.9	0.0	27.5	0.0	

Columns indicate the group niche area being overlapped, e.g., 82.5% of the cyprinids niche is overlapped by benthic cichlids, while 55.1% of the benthic cichlids niche is overlapped by cyprinids.

TABLE 5 | The core isotopic niche area (SEAc) and percent overlap between (A) tilapiine cichlid species and (B) predatory fish species in Lake Liambezi in 2011.

(A)	**SEAc**	***O. andersonii***	***O. macrochir***	***C. rendalli***	***T. sparrmanii***
O. andersonii	8.9		35.7	0.1	12.0
O. macrochir	4.2	16.9		0.0	0.0
C. rendalli	11.4	0.1	0.0		49.6
T. sparrmanii	8.1	10.9	0.0	35.3	

(B)	**SEAc**	***C. gariepinus***	***C. ngamensis.***	***S. intermedius.***	***S. macrocephalus***	***H. cuvieri***
C. gariepinus	2.73		0.0	3.7	31.7	42.7
C. ngamensis	3.41	0.1		42.2	0.0	6.1
S. intermedius	5.83	7.9	72.1		11.6	0.0
S. macrocephalus.	5.77	67.0	0.0	11.5		50.3
H. cuvieri.	3.55	55.7	6.4	0.0	31.0	

crustacea and fish had similar contributions, followed by insect eggs.

DISCUSSION

Primary Production Sources Supporting Fishes

Stable isotopic values of POM indicated that it was composed primarily of freshwater phytoplankton (see Cloern et al., 2002; O'Reilly et al., 2002; Harding and Hart, 2013; Morana et al., 2015) and was clearly the primary carbon source supporting consumer biomass in Lake Liambezi, however substantial contributions from aquatic macrophytes (including associated detritus and periphyton), the most conspicuous source of primary production in the lake, were also present. This highlights the importance of algal (here phytoplankton and/or periphyton) carbon in aquatic food webs, even when aquatic macrophytes are the dominant primary producers (Araujo-Lima et al., 1986; Forsberg et al., 1993; Lewis et al., 2001; Herwig et al., 2004). Terrestrial C_3 macrophytes can also be important carbon sources in aquatic food webs (e.g., Berggren et al., 2014), particularly when algal growth is light limited (Zeug and Winemiller, 2008; Roach and Winemiller, 2015). However, the probability of a substantial contribution of terrestrial carbon in Lake Liambezi, except during the filling phase, was deemed small due to the large surface area of the lake relative to its circumference, and because benthic fish are not restricted to nearshore areas that would receive greater terrestrial carbon inputs. This differs considerably from riverine food webs which in this region are supported mainly by riparian vegetation from the floodplains and detritus from aquatic macrophytes (Taylor et al., 2017b).

Trophic Pathways

Carbon from phytoplankton and aquatic macrophytes was assimilated into the food web via three major pathways, one pelagic and two benthic. These are summarized visually in **Figure 6**.

In the pelagic food web phytoplankton was assimilated directly by herbivorous zooplankton, such as calanoid copepods (Grosbois et al., 2017b) or cladocerans (e.g., *Bosmina longirostis*, Seaman et al., 1978) that are preyed upon by larger zooplankton, such as cyclopoid copepods and chaoborid larvae, as well as small zooplanktivorous fishes that include the poecilid *Micropanchax johnstonii* and the alestids *B. lateralis* and *R. maunensis*. Stomach content analysis showed that zooplankton and Diptera larvae (aquatic invertebrates) made up a large portion of the diet of *B. lateralis*, yet while isotope data generally supported these observations, the $\delta^{15}N$ values revealed that *B. lateralis* and zooplankton occupied the same trophic level. This may be

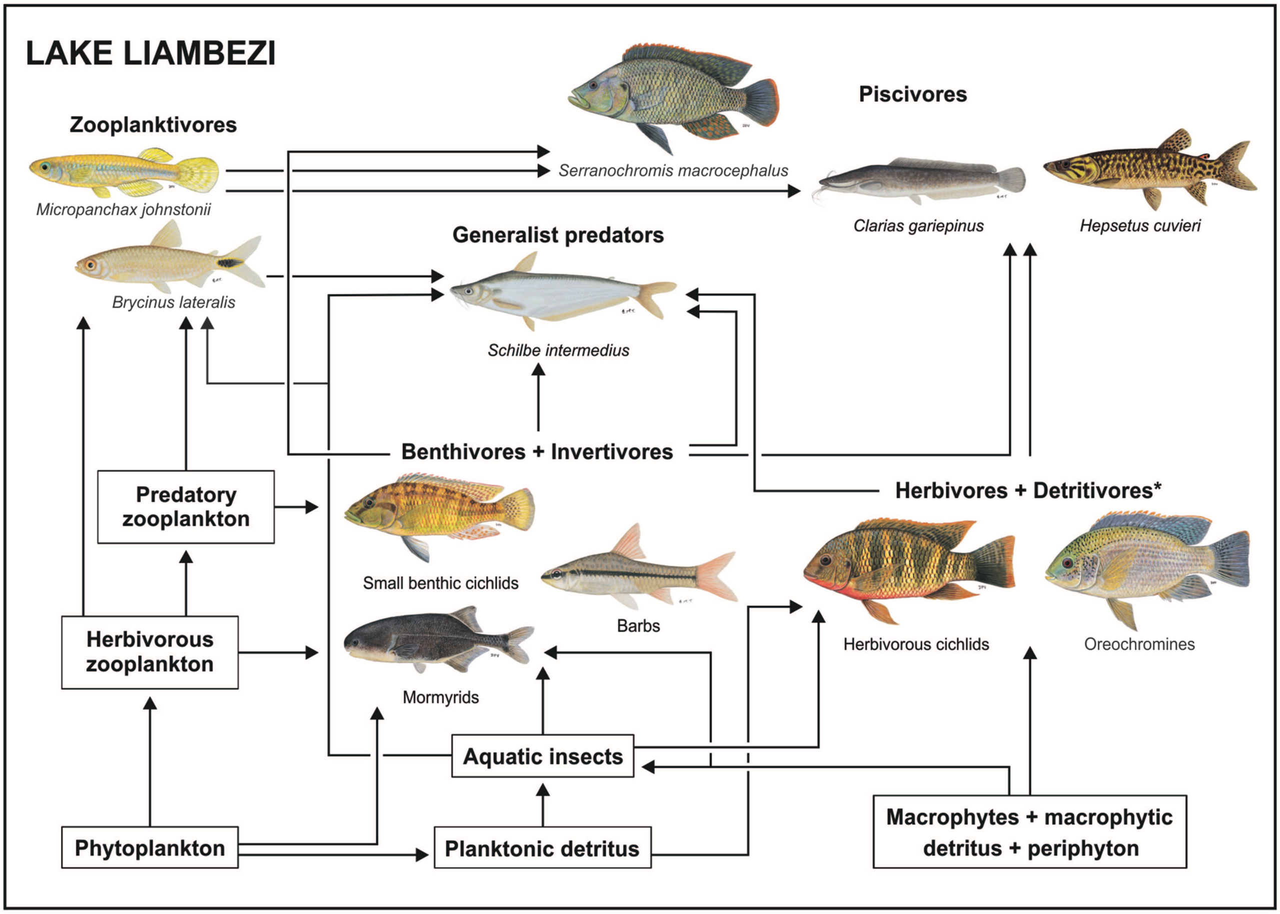

FIGURE 6 | Conceptual diagram of the food web in Lake Liambezi, illustrating the flow of energy through three major food chains, and their integration by generalist predators and piscivores in the mature lacustrine fish community. *Herbivores and detritivores incorporate all the tilapiine cichlids. All fish images are ©NRF-SAIAB.

due to several factors including different tissue turnover rates among species, variable $\delta^{15}N$ values among sampling periods, and seasonal variation in the abundance of zooplankton and dipteran larvae and/or their importance in the diet of *B. lateralis,* as seasonal variation in diet is well-documented for *Brycinus* species (e.g., Booth and McKinlay, 2001).

Thus, the second major pathway by which basal carbon was assimilated into the food web was via aquatic invertebrates that feed primarily on detritus of planktonic origin or potentially on emergent macrophytes and associated macrophytic detritus and/or periphyton. Among the most important aquatic invertebrates in Lake Liambezi are diptera larvae, ephemeroptera, trichoptera, and odonata nymphs (Seaman et al., 1978). These support benthic invertivorous mormyrids, cichlids, barbs, and to a lesser degree, generalist predators, such as *S. intermedius*. The mormyrids *Petrocephalus* cf. *okavangensis* and *Marcusenius altisambesi* are some of the most specialized insectivorous fishes in Lake Liambezi and feed primarily on the dominant aquatic insect groups mentioned above (van der Waal, 1985; Winemiller and Adite, 1997), but also showed a reliance on POM and submerged plants in the mixing models. The benthic invertivore cichlid group comprised four species, the small sized *P. acuticeps* and *Pseudocrenilabrus philander*, and two medium sized *Sargochromis* species. The diets of these cichlids were more diverse and flexible than those of the mormyrids (van der Waal, 1985; Winemiller, 1991; Zengeya and Marshall, 2007), incorporating substantial contributions from all available food resources. As members of this group are important prey species of the top piscivores (**Table 2**), they play an important role in moving energy up the food web.

The third major pathway involves the tilapiine cichlids which include *O. andersonii*, *O. macrochir, T. sparrmanii* and *C. rendalli*. This group occupies the lowest trophic level of all the fish in the lake, indicating that they were largely primary consumers. The isotopic positioning of the tilapiine cichlids indicated reliance on POM (particularly in 2012) as well as on submerged (in 2011) and emergent plants (2012) and/or detritus. *Coptodon rendalli* is regarded as being a specialized macrophyte feeder (van der Waal, 1985; Winemiller and Kelso-Winemiller, 2003) which is consistent with the relatively high average $\delta^{13}C$ values and supports the mixing model which showed a reliance on submerged plants, filamentous algae, detritus and

POM. *Tilapia sparrmanii* incorporated large contributions of POM into its diet, along with smaller amounts of zooplankton, aquatic invertebrates and submerged plants. In 2011, the isotopic niche of *T. sparrmanii* overlapped with that of *C. rendalli* by approximately one third, supporting mixing model results and previous dietary observations that *T. sparrmanii* consume a small amount of aquatic macrophytes (van der Waal, 1985; Winemiller and Kelso-Winemiller, 2003; Zengeya and Marshall, 2007). The higher average δ^{15}N value over other tilapiine cichlids suggests that *T. sparrmanii* is likely more omnivorous, feeding at multiple trophic levels, which is supported by van der Waal (1985) who recorded a variety of aquatic and terrestrial invertebrates, fish remains and zooplankton in the diet of *T. sparrmanii* in the lake. Data from 2011 also showed that the larger *Oreochromis* species had lower δ^{15}N values, and shared little isotopic niche space with *C. rendalli* and *T. sparrmanii, whereas Oreochromis andersonii* had a similarly wide δ^{13}C range to that of *C. rendalli* but was on average 4‰ more depleted. Mixing models suggested a reliance on POM in both years, as well as submerged macrophytes in 2011. *Oreochromis andersonii* with lower δ^{13}C values were probably more reliant on algal carbon sources, while those with higher δ^{13}C values probably consumed more detritus derived from the abundant aquatic macrophytes, demonstrating some degree of individual specialization (Gu et al., 1997; Benhaïm et al., 2017). In contrast, *O. macrochir* occupied a small isotopic niche, and a lower trophic position than *O. andersonii,* although mixing models suggested they also fed on POM, detritus and submerged plants (2011) as well as POM and filamentous algae (2012). The low levels of dietary overlap support observations by van der Waal (1985) who identified algae and zooplankton as the most important food sources for *O. andersonii* and fine detritus as the main food source for *O. macrochir*. Of note is that the tilapiine cichlids, despite being the backbone of the Lake Liambezi fishery, accounted for a minimal proportion of this study's CPUE. This is likely indicative of strong fishing pressure in Lake Liambezi, where subsistence fishers are capable of removing substantial biomass (i.e., 27 00 t/year in 2011–2012; Peel et al., 2015).

Integrating Trophic Pathways

While the three trophic pathways discussed above are by no means discrete (fishes may forage across pelagic and benthic food chains), predators occupying the highest trophic levels fully integrate all pathways (Vander Zanden and Vadeboncoeur, 2002). The dominant predator in Lake Liambezi in terms of biomass was *S. intermedius* (**Supplementary Table 1**; Peel et al., 2015, 2019), a generalist predator, which consumed a wide variety of prey items including fish, aquatic and terrestrial invertebrates, decapods and gastropods. The broad, but fish-dominated diet of *S. intermedius* observed during the present study was consistent with previous observations from Lake Liambezi (van der Waal, 1985) and with dietary (Merron and Mann, 1995; Winemiller and Kelso-Winemiller, 1996) and trophic (Taylor et al., 2017b) assessments in neighboring rivers. *Schilbe intermedius* shared a significant amount of isotopic niche space with *C. ngamensis*, which also feeds on a wide variety of fish, insects, molluscs, and decapods (Willoughby and Tweddle, 1978; van der Waal, 1985; Winemiller and Kelso-Winemiller, 1996). These two species occupied a lower trophic position than the top predators, overlapping more with benthic cichlids, cyprinids and mormyrids.

Stomach contents and stable isotope analysis revealed a significant level of dietary overlap among the three piscivores *C. gariepinus*, *H. cuvieri* and *S. macrocephalus*. *Clarias gariepinus* and *H. cuvieri* fed almost exclusively on cichlids, while *S. macrocephalus* fed predominantly on alestids. Although *C. gariepinus* is known to have a broad omnivorous diet (Willoughby and Tweddle, 1978; Bruton, 1979; van der Waal, 1985; Winemiller and Kelso-Winemiller, 1996), they often specialize on a fish prey (Merron, 1993; Weyl et al., 2016). Stable isotope analysis provided strong support for the high contribution of both benthic and tilapiine cichlids to the diets of *C. gariepinus* and *H. cuvieri*, and clearly illustrated how these species integrated the two benthic trophic pathways described above. Variation in trophic position of individual *C. gariepinus* and *H. cuvieri* suggests some degree of specialization. Individuals with depleted δ^{13}C values had high trophic positions, reflecting the greater number of trophic transfers involved in obtaining energy from omnivorous and insectivorous benthic cichlids. Individuals with enriched δ^{13}C values had lower trophic positions, as fewer trophic transfers were involved in obtaining energy from the detritivorous and herbivorous tilapiine cichlids. *Serranochromis macrocephalus* were, on average, slightly more enriched in δ^{15}N and depleted in δ^{13}C compared to *C. gariepinus* and *H. cuvieri*, as they fed more evenly across all three trophic pathways indicating a more diverse diet than the alestid-dominated gut content analysis would suggest. As a result, *B. lateralis* the most abundant species in the lake (Peel et al., 2015), appears relatively poorly utilized as a prey resource and its occupation of the pelagic food web may be facilitated by predator release.

The use of the pelagic food chain, even if on a small scale, by *B. lateralis* may well have been facilitated by the absence of *Hydrocynus vittatus*, a large pursuit predator, from the lake (Peel et al., 2015). Where it occurs, *H. vittatus* exerts top-down control on fish communities, restricting smaller fishes to shallow littoral refugia and to macrophyte beds (Jackson, 1961). Comparing the food web of Lake Liambezi with that developed by Taylor et al. (2017b) for the upper Zambezi River demonstrates this idea (**Figure 7**). While the Zambezi River fish community is richer because it includes several species that were unable to colonize Lake Liambezi, zooplanktivory is only represented by *M. johnstonii*, a small poecilid that is strongly associated with aquatic vegetation (Skelton, 2001). In the Zambezi River *B. lateralis* occupies a benthic insectivore niche (**Figure 7**). This is different to Lake Liambezi, where we propose that, in the absence of *H. vittatus* resulted in predation release which facilitated the use of pelagic space by *B. lateralis* allowing it to make use of an unexploited niche and exit the more competitive food chain driven by benthic invertebrates.

In summary, the investigations into trophic and food web structure supports the hypothesis that phytoplankton production supports a high amount of consumer biomass in Lake Liambezi, however substantial contributions by periphyton/emergent plants are also likely. These results add to the large body of evidence highlighting the importance of algal production

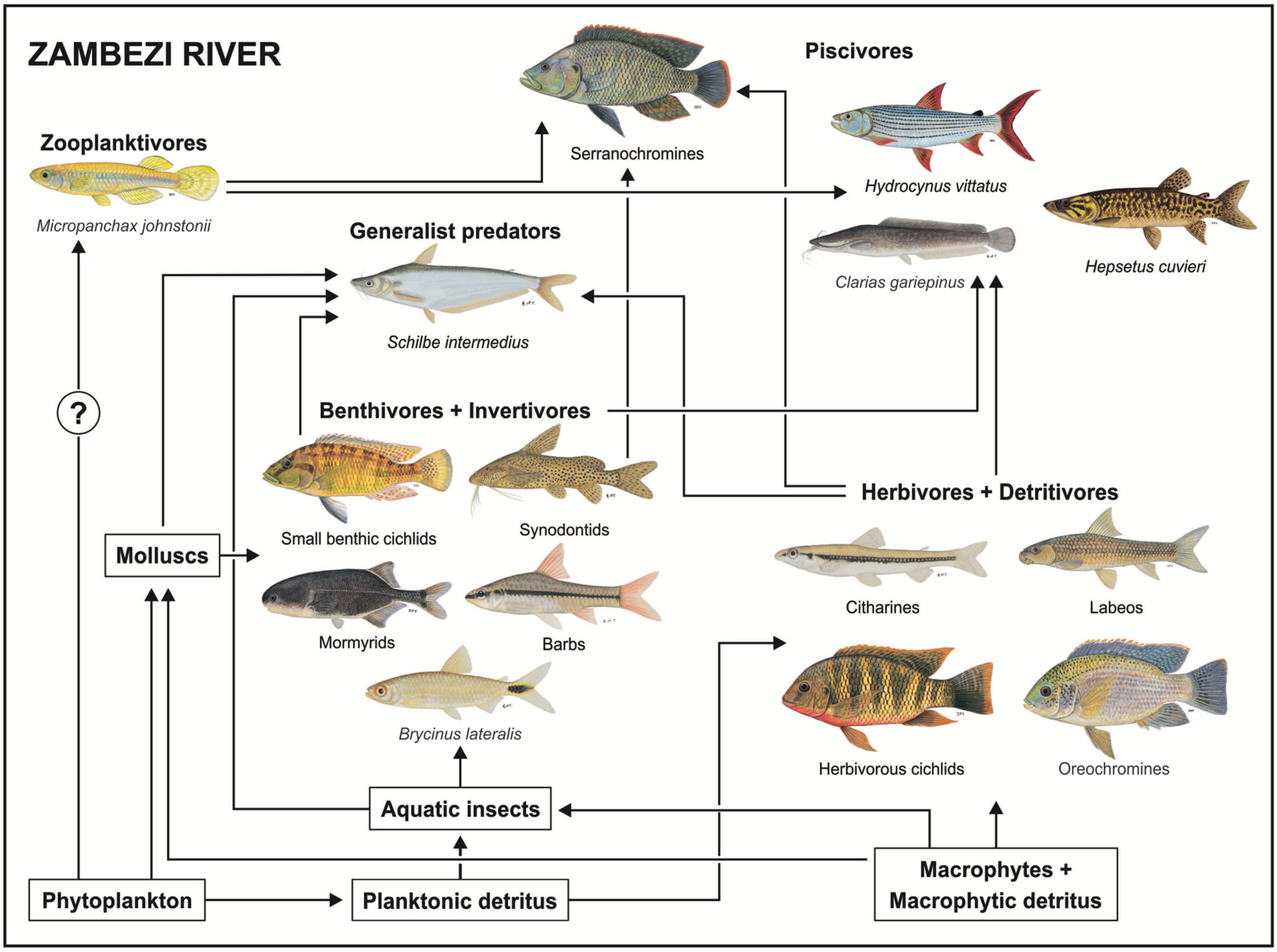

FIGURE 7 | Conceptual diagram of the food web in the Zambezi River as described by Taylor et al. (2017b), illustrating the flow of energy through three major food chains, and their integration by generalist predators and piscivores in the riverine fish community. All fish images are ©NRF-SAIAB.

sources to fishes, even where macrophytes appear to be the dominant source of primary production (Winemiller, 2004; Douglas et al., 2005). Submerged and emergent macrophytes (including associated detritus and potentially periphyton) do however, contribute to the assimilated diets of the tilapiine cichlids, which are the mainstay of the commercial gillnet fishery on the lake (Peel et al., 2015). Of the three major food chains, the phytoplankton based pelagic food chain was longest. The benthic food chain based on detritus of planktonic origin was characterized by high levels of omnivory and the macrophytic detritus-based food chain was shortest. Predators fed across all three food chains, but more so on the two benthic food chains. A combination of dietary overlap, dietary specialization, the integration of multiple food chains and the behavioral adaptation to changing dietary resources, underpins the ability of Lake Liambezi's fish community to thrive under the stochastic nature of ephemeral ecosystems. Unfortunately, the development of a substantial subsistence tilapiine fishery on Lake Liambezi (Peel et al., 2015, 2019) combined with the recession of lake water after 2014 resulted in the collapse of the cichlid fishery in 2016 (Peel et al., 2019; Tweddle, personal observation). The management of Lake Liambezi during its next cycle of inundation should likely focus on monitoring size and abundance of fish species involved in the longer phytoplankton based pelagic food chain, as its length and complexity would contribute to ecosystem stability. Management of catch quotas and acceptable fishing gears may also be needed in future to prevent fishery collapse (and its knock-on economic effects on subsistence livelihoods, see Simasiku et al., 2017) before the start of the subsequent drying cycle.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by South African Institute for Aquatic Biodiversity Animal Ethics Committee.

AUTHOR CONTRIBUTIONS

RP and OW: ideas, data collection, analysis, manuscript preparation, and funding. JH: ideas, analysis, and manuscript preparation. GT: ideas, data collection, and analysis.

FUNDING

This research collaboration was facilitated by a South African–Namibia Research Partnership Programme Grant (National Research Foundation NRF Grant No.: UID 74015). Fieldwork was funded through the Namibia Nature Foundation (NNF) managed Integrated Community-Based Ecosystem Management (ICEMA) Project, the Nedbank Namibia Go-Green Fund, the Southern African Science Service Center for Climate Change and Adaptive Land Management (SASSCAL), NNF/WWF Zambezi/Chobe Fisheries Project, the EU/NNF Community Conservation Fisheries in KAZA project, Rhodes University, Department of Environmental Affairs: National Resource Management Programme, Working for Water Programme, and the South African Research Chairs Initiative of the Department of Science and Technology (Grant No. 110507).

ACKNOWLEDGMENTS

We gratefully acknowledge the Ministry of Fisheries and Marine Resources, Namibia, for granting permission to carry out this research and for providing technical and logistic support. We acknowledge use of infrastructure and equipment provided by the SAIAB Research Platform and the funding channelled through the NRF-SAIAB Institutional Support system. Special thanks to Denis Tweddle for logistical, technical and intellectual support. Thank you to Susan Abraham for drawing our stylized food web diagrams

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2019.00192/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 22 January 2020
doi: 10.3389/fenvs.2019.00207

Socio-Economic Determinants of Land Use/Cover Change in Wetlands in East Africa: A Case Study Analysis of the Anyiko Wetland, Kenya

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In East Africa, wetlands are steadily converted to agriculture for food security reasons. This study analyzed high spatial resolution panchromatic and color photographs in the Anyiko wetland in Kenya to reveal wetland conversions between 1966 and 2018. In addition, socio-economic determinants of land use/cover change are assessed in the Anyiko wetland. Socio-economic data was collected through a questionnaire survey of 226 households. A Chi-squared Automatic Interaction Detector (CHAID) decision tree approach is utilized to assess determinants of wetlands conversion. The results showed that between 1966 and 2018, the wetland area reduced by 55%, mostly attributed to agricultural development. Households were more likely to cultivate the wetland if they did not harvest papyrus for artisanal products, were male-headed and lacked alternative sources of income. The perceptions that wetland is "wasteland" and conversion to agriculture provides higher net monetary benefit did not influence wetland cultivation. Hence, the conversion of the wetland was determined by the socio-economic status of the households rather than perceptions on its value.

Keywords: CORONA, ecosystem services, agriculture, livelihoods, wetlands

Edited by:
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Specialty section:
This article was submitted to Land Use Dynamics, a section of the journal Frontiers in Environmental Science

Received: *03 October 2019*
Accepted: *31 December 2019*
Published: *22 January 2020*

Citation:
Ondiek RA, Vuolo F, Kipkemboi J, Kitaka N, Lautsch E, Hein T and Schmid E (2020) Socio-Economic Determinants of Land Use/Cover Change in Wetlands in East Africa: A Case Study Analysis of the Anyiko Wetland, Kenya. Front. Environ. Sci. 7:207. doi: 10.3389/fenvs.2019.00207

INTRODUCTION

Wetlands provide a wide range of ecosystem services (ESS) including provisioning (e.g., food, fresh water, biochemicals, genetic materials, fiber, and fuel), regulating (e.g., climate regulation, water purification and waste treatment, erosion and flood control), supporting (e.g., primary production, nutrient cycling, and soil formation), and cultural services (e.g., recreation, aesthetics, education, spiritual, and religious values) (MEA, 2005; Russi et al., 2013). These ESS are not only important in supporting livelihoods, but also human well-being (MEA, 2003, 2005). The significance of the ESS, however, vary between temperate and tropical regions (Rebelo et al., 2013). In tropical regions, wetlands mainly serve for provisioning ESS, spiritual and biodiversity purposes, and for biodiversity, recreational and educational purposes in temperate regions. Despite the importance of these ESS to many people, wetlands continue to be degraded and have been identified as one of the most threatened ecosystems globally (MEA, 2005). This is majorly attributed to drainage and conversion to agricultural land and increased withdrawal of water due to economic development and food demand (MEA, 2005). For instance, it is estimated that more than 50% of specific types of wetlands (i.e., coastal and inland marshes, peatlands, and emergent estuarine) in parts of North America, Europe, Australia, and New Zealand were converted to agriculture during the twentieth century while elsewhere, many estimates are speculative as reliable data is missing (Finlayson et al., 2005; MEA, 2005; Rebelo et al., 2009).

In sub-Saharan Africa, the use of wetlands for agricultural production is increasingly considered as a potential solution to food security challenges in the region (UNEP, 2008; Rebelo et al., 2010). According to Sakané et al. (2011), wetlands are characterized by nutrient rich-soils with high moisture contents, enabling smallholder farmers to produce crops all year round. Over the last decades, this potential has been progressively exploited by smallholder farmers as demand for food rises due to economic and demographic growth, climate change and decline in agricultural productivity of terrestrial landscape (Dixon and Wood, 2003). In East Africa, wetlands provide 10–40% of the annual food needs of the rural population (Schuyt, 2005). During periods of food shortage, wetlands can be the exclusive source of food for communities living around them (Rebelo et al., 2010). However, many wetlands in sub-Saharan Africa are increasingly being degraded and lost due to agricultural expansion by drainage and conversion (Dixon, 2002; Schuyt, 2005; Owino and Ryan, 2007; Rebelo et al., 2010; Adekola et al., 2012; Saunders et al., 2012). For instance, in Uganda, NEMA (2010) estimates that between 1999 and 2008, agricultural expansion in wetland areas averaged 410 ha/year. In Kenya, Owino and Ryan (2007) report 50% area loss in some papyrus wetlands over the period 1969–2000. Though these conversions of wetlands to cropland may enhance food provisioning ecosystem service in short term, regulating ESS may decline in the long term (Foley et al., 2005; Van Dam et al., 2013).

Inadequate understanding of wetland values to stakeholders due to lack of readily available data and information has been recognized as a major reason why wetlands conversions to other land uses take place (Schuyt, 2005; Mmopelwa, 2006). Traditionally, wetlands are perceived as "wastelands" and hence "such apparent waste can only be put to good use, if they are reclaimed for agriculture or human settlement" (Maltby, 2013, p. 9). When not considered as "wastelands," wetlands are commonly perceived to have minimal value in comparison to other uses of their land that may produce more tangible, immediate and higher monetary benefits (Schuyt, 2005). Jogo and Hassan (2010), however, argue that although there is increased awareness on the values of wetlands, degradation and land use change continue to occur. This is evident in several case studies in East Africa such as Nakivubo wetland in Uganda (Emerton et al., 1999; Kansiime and Nalubega, 1999; Isunju and Kemp, 2016), Nyando and Yala wetlands in Kenya (Schuijt, 2002; Kipkemboi et al., 2007; Onywere et al., 2011; Khisa et al., 2013; Oduor et al., 2015). The conversion to agriculture is not only initiated by the local people, but also by governmental programmes (Swallow et al., 2007; Nabahungu and Visser, 2011). Hence, not only the perceptions of smallholders about wetlands and their monetary benefits in comparison to conversion to agriculture are important, but also other socio-economic determinants contributing to their conversion.

Studies explicitly quantifying spatio-temporal extents of wetlands encroachment by human activities in sub-Saharan Africa are limited (Mwita et al., 2013; Isunju and Kemp, 2016). Understanding the linkages between wetlands conversion to agriculture and socio-economic determinants including households' perceptions on their values is important. Therefore, this study analyzed socio-economic determinants of land use/cover change in wetlands at household level using the Anyiko wetland in Kenya as a case study. The objectives of this study were to: (1) determine spatio-temporal change of agriculture in the wetland, and (2) analyze socio-economic determinants of wetland utilization for agriculture. The land use/cover change in the wetland was analyzed by visual interpretation of high spatial resolution panchromatic and color photographs for 1966 and 2018, respectively. A household survey was conducted to gather information on household characteristics, wetland utilization status and perceptions on the ecosystem's value. A Chi-squared Automatic Interaction Detector (CHAID) decision tree analysis was performed to statistically examine the determinants influencing conversion of Anyiko wetland to agriculture.

The next section of the article describes the study site, land use/cover data and processing, household data collection, and the methods used for analyzing land use/cover change in the wetland and socio-economic characteristics influencing wetland use and households' perceptions. This is followed by results which are discussed, and conclusions drawn in the last section.

MATERIALS AND METHODS

Description of the Anyiko Wetland

The Anyiko wetland is a permanent papyrus (*Cyperus papyrus*) dominated inland wetland in Ramunde and Sihayi sub-locations (administrative regions) of Siaya county in Kenya (**Figure 1**). The wetland covers an area of $\sim$1 km^2 and is situated within longitudes 34°16′30″E and 34°18′0″E and latitudes 0°16′0″N and 0°14′30″N in Nzoia River basin, which is the largest (12,696 km^2) sub-basin of Lake Victoria in Kenya (MEMR, 2012). The wetland lies at an altitude between 1,050 and 1,300 m above sea level. It is fed by streams and springs and drains into the Nzoia River. Before drainage and conversion to agriculture, the wetland extended up to Jera sub-location.

The former and current wetland areas are surrounded by 18 villages consisting of 760 homesteads. The current (2017/18) number of households in the homesteads and population of people in the villages are not documented. The villages bordering the wetland downstream use the ecosystem mainly for rice irrigation and production, and papyrus mats production, while those upstream, obtain papyrus fiber, papyrus mats, and engage in vegetables, yams, and maize production. These provisioning ESS derived from the former and current wetland areas are used for subsistence and commercial purposes.

Anyiko wetland experiences a bimodal rainfall pattern with long rains in March-May and short rains in September-November. The average annual rainfall in the area is 1,556 mm and ranges from 813 to 2,417 mm annually with a minimum

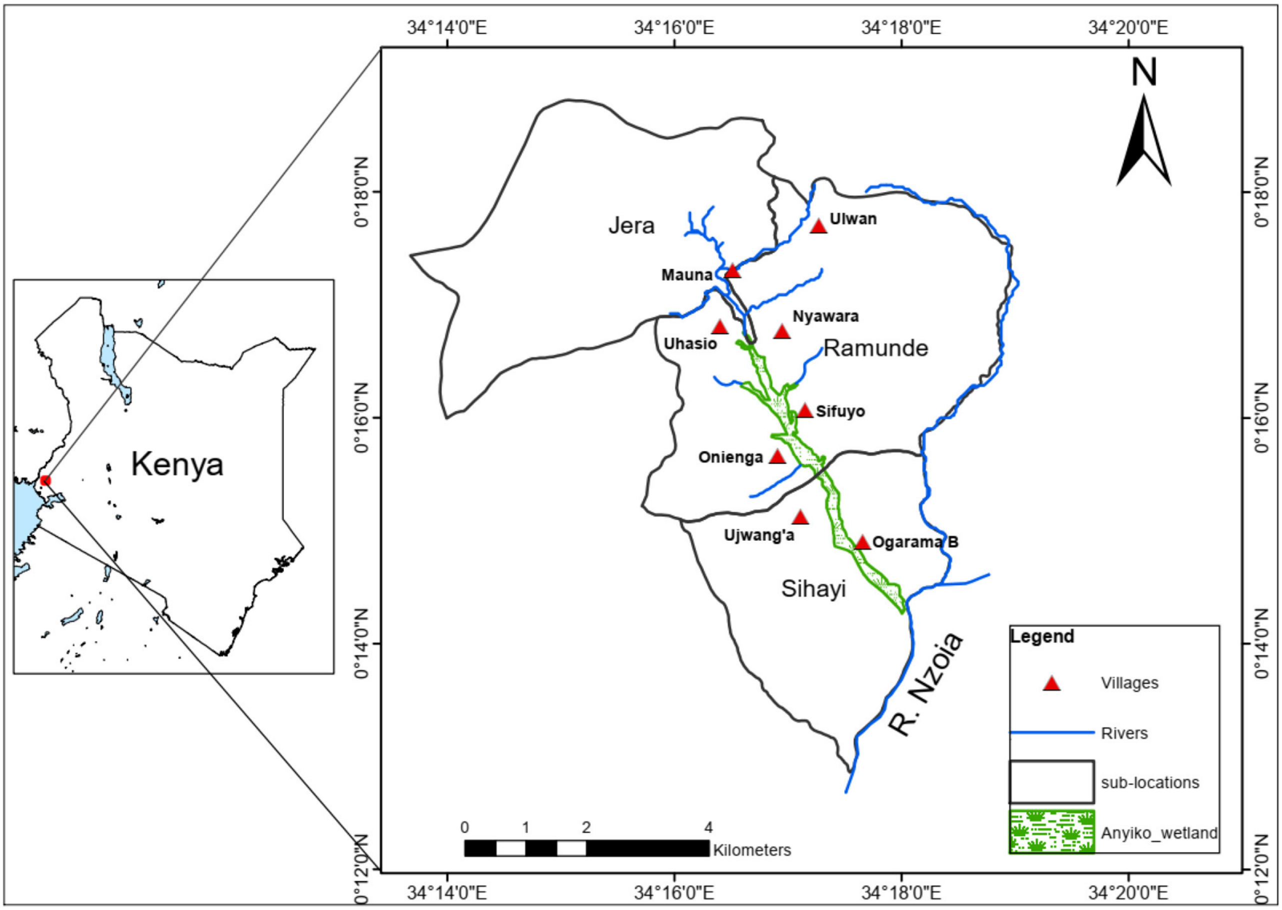

FIGURE 1 | Map showing location of the Anyiko wetland and the villages sampled.

monthly rainfall of 40 mm and maximum of 231 mm (data based on Uholo weather station for the last 10 years (2007–2017). Generally, the average temperature in the area is 22°C with a maximum temperature of 30°C and minimum of 15°C (Climate-Data.org, n.d.).

Land Use/Cover Change in Anyiko Wetland

Data Acquisition, Processing and Analysis

Land use/cover change analysis is commonly achieved using satellite imagery such as the U.S. Geological Survey (USGS) Landsat satellite image data. However, due to the relatively low spatial resolution (60 m ground sampling distance for Landsat-2 and 30 m for Landsat-8) coupled with papyrus harvesting and dry season burning in the wetland, it was difficult to differentiate between the natural vegetation and crops farmed in the wetland. This implied that using the traditional pixel-based algorithms for automatic image classification and Landsat-like observations may lead to misclassification problems. High spatial resolution panchromatic photographs and color satellite image data for 1966 and 2016/18, respectively, were therefore used to quantify the spatiotemporal patterns of agricultural expansion in the Anyiko wetland.

A cloud-free panchromatic photograph of the wetland and its surrounding taken on 17th November 1966 was acquired from CORONA KH-4A declassified data. CORONA is the code name for a classified military satellite system launched successfully in space from the 1960s for reconnaissance and production of maps for U.S. intelligence agencies [USGS (n.d.)]. CORONA and other military satellite systems, such as ARGON and LANYARD data collected on Earth's surface between 1960 and 1972 were declassified by Executive Order 12,951 in 1995. This was because the images were no longer crucial to the U.S. national security and were likely of historical importance to global change study. The satellite photograph "DS1037-2138DA010" used in this study was published on 1st January 1995 by USGS Earth Resources Observation and Science (EROS) Center. The image frame, film type and ground resolution were 10, 70 mm Panoramic and 3 m, respectively.

The 1966 CORONA photograph was obtained as a digital image file and geo-referenced to the Google Earth data using a series of ground control points with a 1st order polynomial transformation. Using visual interpretation of the landscape in which the wetland was situated, the borders of the wetland and its surrounding were manually digitized from the 1966 image data. Polygons of different land use/cover occurring continuous in an area ≥1 acre (minimum mapping unit) were labeled into four land use/cover categories: wetland, wetland/close shrubland, open shrubland, and close shrubland. Characteristics used in the interpretation of the landscape included: pattern, size, texture, tone/color, association, and shape.

An image composite available in Google Earth at 0.5 m spatial resolution was used for 2018. The image data were taken on 13th June 2016 and 28th December 2018. The 1966 land use/cover vector map was overlaid on the 2016/18 image to update individual polygons through visual image interpretation. For the 2016/18 period, the land use/cover types were categorized into: wetland, farmland, close shrubland and open shrubland.

To estimate area covered by each land use/cover type for 1966 and 2016/18 periods, all polygons belonging to the same land use/cover category were selected using a spatial query function implemented in ArcGIS (ESRI). The total area (in acres) for the selected polygons were determined for each year. This was repeated for polygons belonging to other land use/cover types for both years. Land use/cover changes between 1966 and 2016/18 were calculated. Interclass conversions were calculated for 1966 and 2016/18 to quantify wetland extent loss or gain to farmland and other land use/cover types. Alluvial diagram showing changes from one land use/cover to another between 1966 and 2016/18 was created using the R package (https://cran.rproject.org/web/packages/alluvial/vignettes/alluvial.html). For other land use/cover types, which encroached the wetland by 2016/18, 1966 and 2016/18 layers were intersected to create a third layer to identify changes.

Wetland Socio-Economic Survey

Data on wetland utilization and households' perceptions on the ecosystem was collected between July and December 2017 by conducting a household survey. A questionnaire consisting of 23 questions were structured into four sections: (1) socio-economic characteristics of the respondent and household, (2) household's wetland utilization for provisioning ESS and the year it started, (3) household's perceptions on the wetland and their monetary benefits in comparison to conversion to agriculture, and (4) household sources of income and annual amount for 2017. The socio-economic characteristics were household size, age of the respondent, level of formal education of the respondent, marital status, gender of the respondent, and the village in which the household is situated. Section two of the questionnaire constituted a list of provisioning ESS derived from wetlands within Lake Victoria basin as indicated in literature and field observation. In the section, the respondents indicated whether their households were deriving the listed provisioning ESS from the wetland and the year they started using the wetland for the ESS. Households' perceptions on the wetland i.e., Anyiko wetland is a "wasteland" and conversion of the wetland to agriculture has a higher net monetary value than when used for papyrus artisanal products e.g., mat production among other provisioning ESS, were assessed using Likert scale (1 = Agree, 2 = Do not know, 3 = Disagree). Whether there was restriction on wetland utilization was also assessed using Likert scale (1 = Agree, 2 = Do not know, 3 = Disagree). Lastly, annual income from households in 2017 was assessed by asking questions on: whether any household member was formally employed, number of months worked and monthly income and whether any household member had other sources of income apart from formal employment such as from informal employment, business, upland crops sale, building rental, land rental, and remittances among others and their monthly or yearly income. As many rural households in Africa do not keep records, we focused on the current year (2017) of income sources and amount.

The questionnaire was pre-tested and afterwards administered face to face to 226 households out of a total of 489 households (339 homesteads) (Kothari, 2004) in eight randomly selected villages: Ujwang'a, Mauna, Ogarama B, Ulwan, Nyawara, Uhasio, Sifuyo, and Onieng'a (**Figure 1**). Village profiles were carried out using focus group discussion with the village heads. The selection ensured that the former and current wetland areas were covered. The respondents targeted with the questionnaire were household heads and in cases where they were not present at time of the interview, they were interviewed later in the day or the following day. The household survey was conducted with the support of respective village heads of the selected villages to ease access to households and prevent conducting the survey beyond the selected villages' boundaries.

In this study, wetlands were assumed to provide alternative sources of income. This was based on the argument that Anyiko wetland is a relatively small wetland ($\sim$1 km^2) and hence, it is impossible to be the main source of income for the neighboring 18 villages and 760 homesteads. From the field observations we know that the local community is involved in small scale business, brick production among other income generating activities. Increasing dependence of local communities on wetlands provisioning ESS both for income generation and subsistence purpose has been reported in larger wetlands such as Nyando wetland in Kenya, which is $\sim$42 km^2 in size (Kipkemboi et al., 2007; Obiero et al., 2012; Khisa et al., 2013). Hence, income from the ecosystem itself were not included. For instance, income from the sale of crops grown in former wetland areas, papyrus mats and fiber. The income was reported in Kenya shillings (KES) and converted to US dollars ($) based on 2017 average exchange rate of 100 KES = 1$.

Data Analysis

Questionnaire responses were coded and analyzed using IBM SPSS statistics 21 (USA). Using a CHAID decision tree model, 12 predictor independent variables were tested against the dependent variable of wetland cultivation status of the households (**Table 1**, see **Supplementary Material** on why the variables were selected). Both, decision tree and binary logistic regression are commonly used as predictive models. The decision tree model was chosen in this study, because some statistical requirements of a binary logistic regression were not met e.g., no multicollinearity (see **Supplementary Material** for the results). These requirements are not relevant for a decision tree model. CHAID decision tree is a non-parametric procedure and therefore, make no assumptions of the underlying data. Unlike logistic regression, the CHAID algorithm explicitly express patterns among variables in a graphical and easily understandable form using the "if-then" logic (Au et al., 2003). The method can also identify the most important predictor of the dependent

TABLE 1 | Description of variables fitted in the model.

Dependent variable
Whether a household uses the wetland for agriculture (1 if yes: 0 if no)

	Independent variable	**Measurements**
1.	Household size	Number of family members in a household
2.	Sex of household head	1 = Male headed, 2 = female headed
3.	Highest level of formal education of the respondent	1 = None, 2 = Primary, 3 = Secondary, & 5 = College
4.	Age of the respondent	Years
5.	Harvesting papyrus	1 = Yes, 2 = No
6.	Household other sources of income	1 = Yes, 2 = No
7.	Household annual income levels	$
8.	Perception that wetland is "wasteland"	1 = Agree, 2 = Don't know, 3 = Disagree
9.	Perception that agriculture has higher net monetary benefit	1 = Agree, 2 = Don't know, 3 = Disagree
10.	No restriction on wetland utilization	1 = Agree, 2 = Don't know, 3 = Disagree
11.	Year wetland utilization started	Year
12.	Household location	Village name

variable (Milanović and Stamenković, 2016). Therefore, the CHAID decision tree model is suitable for identifying stepwise pathways to wetland conversion to agriculture that would otherwise go unnoticed when logistic regression is employed. Decision trees have been applied widely in fields such as customer churn (Hadden et al., 2007) and medical diagnosis (Rodríguez et al., 2016). Studies on determinants of wetland utilization for provisioning ESS particularly in sub-Saharan Africa have commonly applied logistic regression (Mwakubo and Obare, 2009; Taruvinga and Mushunje, 2010; Turyahabwe et al., 2013), probit model (Oladele and Wakatsuki (2008), and multiple linear regression (Kipkemboi et al., 2007).

In this study, Pearson's chi-squared test (χ^2) was used to examine the relationships between the model variables in the terminal nodes. The CHAID analysis was run with parent and child nodes defined at 10 and 8, respectively, and significance set at (α_{merge}, α_{split}, and P-value) ≤ 0.05. Descriptive statistics of the model variables was used to capture mean and percentages of wetland and non-wetland cultivating households. Pearson's chi-squared test was also conducted to assess the linkages between perceptions and the actual use of the wetland, categorized as: agriculture, wetland provisioning ESS, both agriculture and wetland provisioning ESS, and none.

CHAID Decision Tree

A CHAID decision tree is a symbolic learning technique that organizes information extracted from a training dataset in a hierarchical structure composed of nodes and ramifications (Quinlan, 1986). The nodes represent data groups and ramifications are the results of the tests. The CHAID procedure starts by finding independent variables that have a significant association with the dependent variable (Thomas and Galambos, 2004). The algorithm then determines how the independent variables, continuous and/or categorical, best combine to predict a binary outcome based on the "if then" rules. Each independent variable is recursively partitioned into homogenous groups along the path from the root node (dependent variable and entire data set) to the terminal node (the last node without output branch) (Milanović and Stamenković, 2016). The partitioning is based on a series of merging, splitting, and stopping steps based on user-specified criteria. The independent variable having the strongest association (highest CHI-squared value and lowest p-value) with the dependent variable becomes the first segment or branch in a tree. The partitioning continues until no more significant dependence relationships can be found between the dependent variable and the set of predictors.

In the merging step, using each independent variable, the CHAID merges non-significant categories as follows:

1. Perform cross-tabulation of the independent variable with the binary dependent variable.
2. If the independent variable has two categories, go to step six.
3. χ^2-test is performed for each pair of categories of the independent variable in relation to the binary dependent variable using the χ^2 distribution with significance (α_{merge}) set at 0.05. For non-significant outputs, the paired categories are merged.
4. For non-significant tests identified by $\alpha_{\text{merge}} > 0.05$, the paired categories are merged into a single category. For tests reaching significance identified by $\alpha_{\text{merge}} \leq 0.05$, the pairs are not merged.
5. If any category has less than the user-specified minimum segment size, that pair is merged with the most similar other category.
6. The adjusted P-value for the merged categories using a Bonferroni adjustment is utilized to control for Type I error rate.

The splitting step occurs after determination of all possible merges for each independent variable. This step selects which independent variable is to be used to "best" split the node using the algorithm.

1. χ^2-test for independence using an adjusted P-value for each independent variable.
2. The independent variable with the smallest adjusted P-value is split if the P-value less than the user-specified significance split level (α_{split}) is set at 0.05; otherwise the node is not split and is then considered a terminal node.

The stopping step is conducted to assess the tree growing process using the following user-specified stopping rules.

3. If the tree reached the maximum depth as specified by the user, the tree process stops.
4. If the size of a node is less than the user-specified minimum node size, the node will be not split.
5. If the split of a node results in a child node whose node size is less than the user-specified minimum child node size value, the node will not be split.
6. The CHAID algorithm continues until all the stopping rules are met.

RESULTS

Land Use/Cover Change in Anyiko Wetland and Its Surrounding

Comparing the 1966 to 2016/18 images of the wetland and its surrounding, conversion of the wetland, wetland/close shrubland, and open shrubland to farmland was clearly visible (**Figures 2A,B**). The land use/cover types as visually interpreted for 1966 and 2016/18 images are shown in **Figure 2**. In 1966, there was no visible agriculture in the wetland and its surrounding (**Figure 3**). The wetland was extensive but by 2016/18, there was a reduction in size. In addition, the wetland was fragmented into two parts due to conversion to farmland. By 2016/18, farmland occupied an area of 1,070 acres. The Anyiko wetland land cover type reduced by 55%, open shrubland by 51%, closed shrubland by 87%, while wetland/closed shrubland was totally lost (100%) (**Table 2**).

To quantify wetland extent loss or gain to farmlands and other land use/cover types, interclass changes were calculated for 1966 and 2016/18. By 2016/18, about 40% of the original 1966 wetland vegetation was still intact while the largest portion (43%) was converted to farmland, to open shrubland (15%), and to close shrubland (2%) (**Table 3**). Only 2% (18 acres) of open shrubland became wetland based on 2016/18 images. Wetland/close shrubland was converted to farmland (95%) and open shrubland (5%). The wetland and other land use/cover types were majorly converted to farmland over time (**Figure 4**).

Socio-Economic Determinants Influencing Wetland Utilization for Agriculture

Socio-Economic Characteristics of the Respondents and Households

Among the respondents, 58% were females and 42% males. Age distribution of the respondents ranged from 21 to 90 years with an average of 50 years. The marital status of the respondents comprised of 71, 28, and 1% for married, widowed and single, respectively. Most of the respondents had attained primary school education (57%), while those with no formal, secondary, and college education levels were 27, 14, and 2%, respectively. Each household had an average of 5 people with a minimum of 1 person and maximum of 12 people. Among the households, 86% (194 households) were deriving provisioning ESS such as crops, water for irrigation, aquaculture and livestock, papyrus mats and fiber, palm baskets and hats and pasture from the wetland. The remaining households (32 households) had never derived any provisioning ESS from the wetland. Average annual household income for the year 2017 from non-wetland activities was about $ 404 and ranged between $ 0 and $ 9,000. Additional information on the households are in **Supplementary Material**.

Comparing socio-economic characteristics between wetland cultivating and non-cultivating households, the results show that

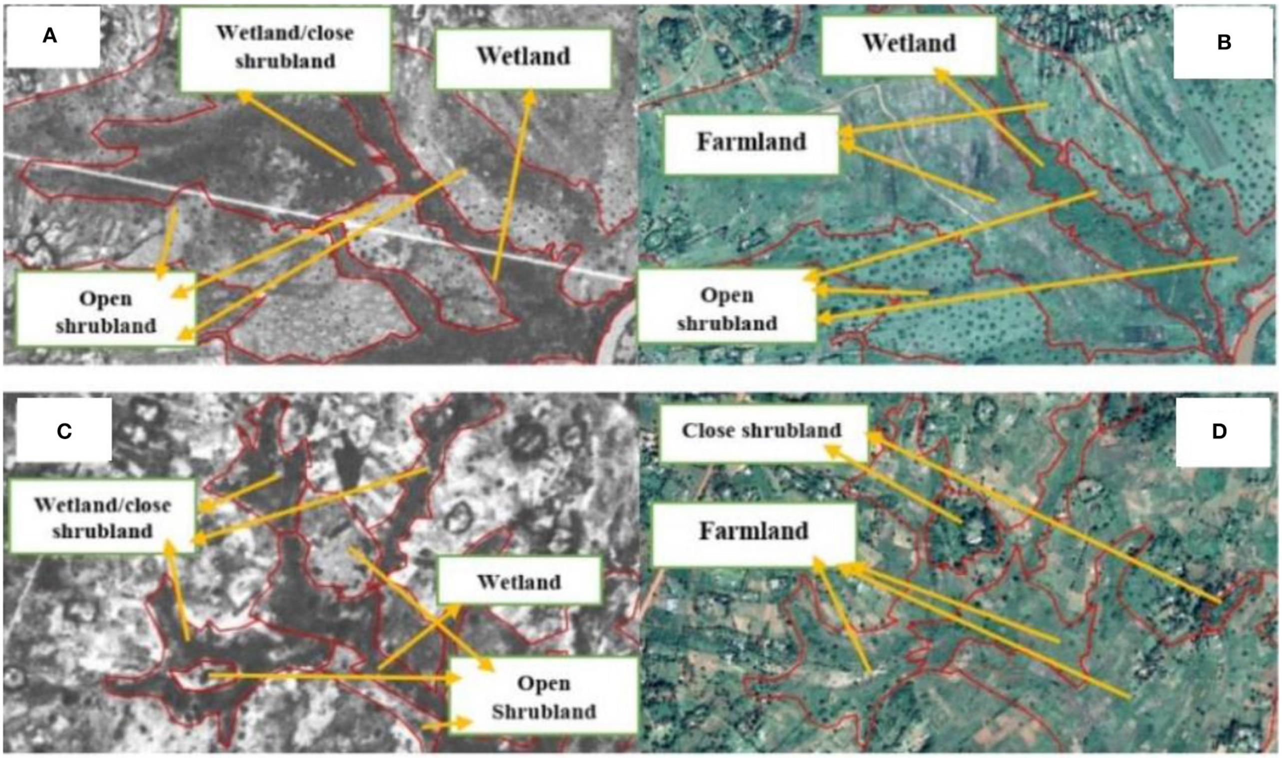

FIGURE 2 | Land use/cover types of the wetland and its surrounding as visually interpreted for CORONA **(A,C)** for 1966 image and Google Earth true color image data **(B,D)** for 2016/18.

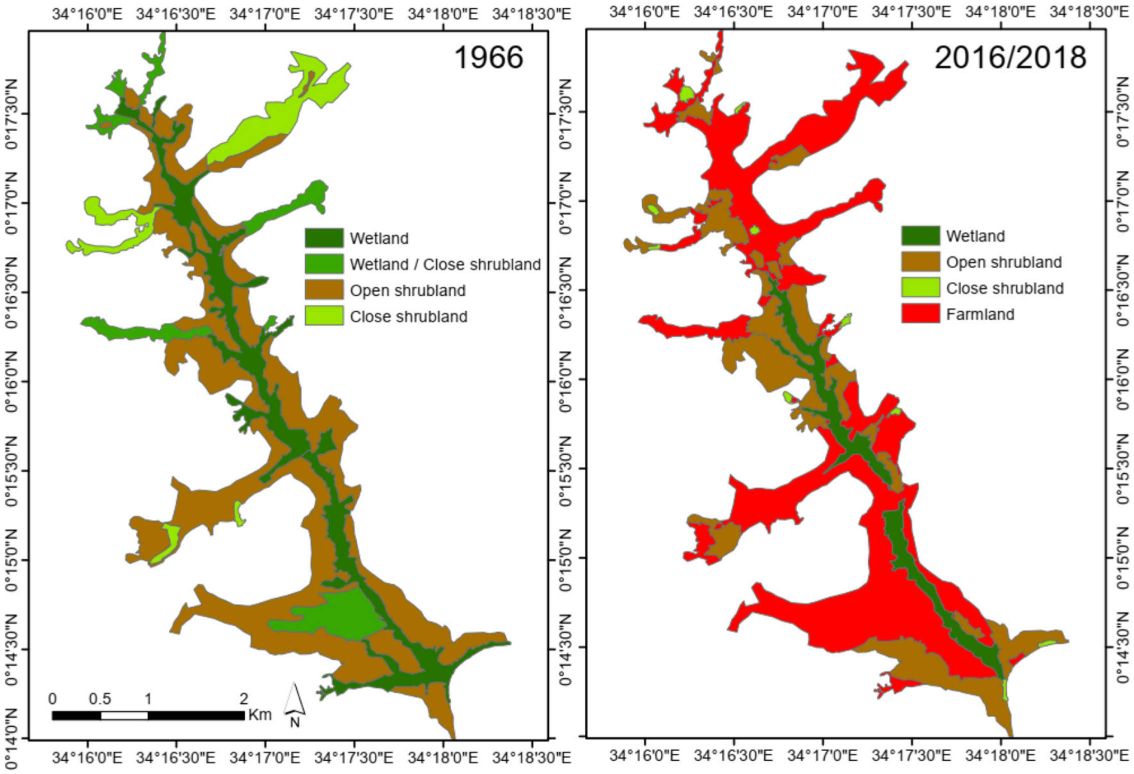

FIGURE 3 | Land use/cover maps of Anyiko wetland and its surrounding in 1966 and 2016/2018.

TABLE 2 | Land use/cover changes in Anyiko wetland and its surrounding between 1966 and 2016/18.

Land cover type	1966	2016/18	Change (1966–2016/2018)	
	Areas (acres)	Areas (acres)	Areas (acres)	Percentage (%) change
Wetland	**390**	**174**	**−216**	**−55**
Open shrubland	999	489	−510	−51
Closed shrubland	170	21	−149	−87
Wetland/closed shrubland	**196**	**0**	**−196**	**−100**
Farmland	**0**	**1,070**	**+1,070**	**+**

The bold values show wetland and farmland coverage in 1966 and 2016/18 and their respective percentage change.

most households cultivating in the former wetland areas were male-headed (80%), did not have alternative sources of income (59%) and were not harvesting papyrus for artisanal products (87%) (**Table 4**).

Determinants of Wetland Utilization for Agriculture

On the CHAID analysis, five predictors: year wetland use started, papyrus harvesting, gender of household head, lack of restriction on wetland utilization and household alternative sources of income reached significance for inclusion in the model (**Figure 5**). Age of the respondent and their highest formal education level, household size, household annual alternative income amount, the perception that wetland is "wasteland," the perception that agriculture has higher net monetary benefit and location (village) of the household did not have a significant effect on wetland utilization for agriculture ($p > 0.05$). Hence, they are not included in further model development. The overall prediction percentage of the model was 84.5% with its ability to predict cultivating and non-cultivating households at 89.7 and 73.5%, respectively.

The tree analysis in **Figure 5** shows a three-level CHAID tree with a total of 17 nodes, of which 10 are terminal nodes. The root node (Node 0) shows that majority, 64% (145 households) of the households surveyed, were cultivating in the former wetland areas. The model identified the year households started using the wetland as a strong predictor in wetland utilization for agriculture ($CHI^2 = 67.51$; df = 4, $p = 0.00$). Five distinct categories of the year wetland use started emerged: ≤1991, 1991–1996, 1996–2012, >2012, and missing. In the period before 1991 to beyond 2012, majority of the households were cultivating in the former wetland areas (**Figure 5**). Contrarily, 88% of the households in the category "missing" were not cultivating in the former wetland areas. CHAID algorithm does not exclude missing data in analysis. The missing data is handled as a separate category which can be combined with other categories if they are statistically homogeneous (Thomas and Galambos, 2004).

TABLE 3 | Inter-class land cover changes (1966–2016/18).

	Land use/cover changes (acres)	**2016/18**				
		Open shrubland (%)	**Wetland (%)**	**Close shrubland (%)**	**Wetland/close shrubland (%)**	**Farmland (%)**
1966	Open shrubland	38	**2**	**1**	0	59
	Wetland	**15**	**40**	**2**	**0**	**43**
	Close shrubland	23	0	2	0	75
	Wetland/close shrubland	5	0	0	0	**95**
	Farmland	0	0	0	0	0

The bold values show the proportion of the wetland that has changed to other land use/cover types and vice-versa between 1966 and 2016/18.

FIGURE 4 | Alluvial diagram showing changes in land use/cover between 1966 and 2016/18.

The households that started using the wetland before 1991 were split into two segments according to the variable "papyrus harvesting" ($CHI^2 = 15.45$; df $= 1$, $p = 0.00$), with one terminal node: households harvesting papyrus (Node 7) and one internal node, households not harvesting papyrus (Node 6) (**Figure 5**). Most (73%) households harvesting papyrus (Node 7) were not cultivating in the former wetland areas. Node 6 was split into two terminal nodes: node 14 and node 15 based on household alternative sources of income ($CHI^2 = 7.39$; df $= 1$, $p = 0.007$), of which 96% of those households not harvesting papyrus (Node 6) and lacked alternative sources of income (Node 14) were cultivating in the former wetland areas.

Households that started using the wetland between 1996 and 2012 (Node 3) were split into two categories: those harvesting papyrus (Node 9) and those not harvesting papyrus (Node 8) ($CHI^2 = 22.69$; df $= 1$, $p = 0.00$) (**Figure 5**). Like the households that started using the wetland before 1991, majority (68%) of the households harvesting papyrus (Node 9) were not cultivating in the former wetland areas. Households not harvesting papyrus (Node 8), of which 87.5% were cultivating in the former wetland areas, were split into two terminal nodes: male-headed (Node 16) and female-headed (Node 17), according to the "gender of the household head" ($CHI^2 = 4.26$; df $= 1$, $p = 0.039$). The results show that 91.5% of the male-headed households (Node 16) were cultivating in the former wetland areas.

Like the households that started using the wetland before 1991 and between 1996 and 2012, majority (96%) of the households that started using the wetland beyond 2012 and were not harvesting papyrus, were cultivating in the former wetland areas ($CHI^2 = 9.74$; df $= 1$, $p = 0.002$) (**Figure 5**). Households categorized as "missing" (Node 5) were split into two terminal nodes: node 12 and node 13 based on the variable "No restriction on utilization" ($CHI^2 = 6.37$; df $= 1$, $p = 0.046$). Both households that agreed (69%) (Node 12) and disagreed/did not know (97%) (Node 13) that there was no restriction on wetland utilization were not cultivating in the former wetland areas (**Figure 5**).

Decision routes to determinants of wetland conversion as presented in **Table 5**, show the "if-then" logic for each of the 10 terminal nodes. The decision routes were subjected to Pearson's chi-squared test to assess the association between the dependent and predictor variables and Boferroni correction to control for Type I error rate (**Table 5**). The decision route of node 0, 1, 6, and 14 show that households that started using the wetland before 1991, did not harvest papyrus for artisanal products and lacked alternative sources of income were significantly more likely to cultivate in the former wetland areas than not ($CHI^2 = 116.11$; df $= 10$, $p < 0.05$; Cramer's V $= 0.72$) (**Table 5**). Contrarily, households that started using the wetland in the same period and harvested papyrus, were less likely to cultivate in the former wetland areas as illustrated in decision route node 0, 1, and 7 ($CHI^2 = 116.11$; df $= 10$, $p < 0.05$; Cramer's V $= 0.72$) (**Table 5**).

Like decision route of node 0, 1, and 7, decision route of node 0, 3, and 9 showed that households that started using

TABLE 4 | Descriptive statistics for selected variables between wetland cultivating and non-cultivating households.

Variables	Cultivating	Not cultivating
AGE OF THE RESPONDENT (YEARS)		
Average	49	52
STDEV	17	17
Maximum	90	84
Minimum	21	23
HOUSEHOLD SIZE (NUMBERS)		
Average	5	4
STDEV	2	2
Maximum	12	11
Minimum	1	1
HOUSEHOLD ANNUAL INCOME		
Average	$ 393	$ 424
STDEV	$ 1,022	$ 1,249
Maximum	$ 6,000	$ 9,000
Minimum	$ 0	$ 0
HIGHEST FORMAL EDUCATION LEVEL OF THE RESPONDENT		
None	24%	33%
Primary	57%	57%
Secondary	17%	7%
College	2%	3%
GENDER OF HOUSEHOLD HEAD		
Male headed	80%	63%
Female headed	20%	37%
HOUSEHOLD OTHER SOURCES OF INCOME		
Yes	41%	58%
No	59%	42%
PAPYRUS HARVESTING		
Yes	13%	36%
No	87%	64%
YEAR WETLAND USE STARTED		
≤1970	6%	13%
1971–1980	9%	7%
1981–1990	10%	21%
1991–2000	26%	11%
>2001	49%	48%
PERCEPTION THAT WETLAND IS "WASTELAND"		
Agree	47%	52%
Don't know	7%	11%
Disagree	46%	37%
PERCEPTION THAT AGRICULTURE HAS HIGHER NET MONETARY BENEFIT		
Agree	61%	58%
Don't know	21%	14%
Disagree	18%	28%
NO RESTRICTION ON WETLAND UTILIZATION		
Agree	66%	77%
Don't know	4%	5%
Disagree	30%	18%

the wetland between 1996 and 2012 and harvested papyrus for artisanal products were significantly less likely to cultivate in the former wetland areas ($CHI^2 = 116.11$; df = 10, $p < 0.05$; Cramer's V = 0.72) (**Table 5**). Contrarily, in the same period (Node 3), households that did not harvest papyrus for artisanal products (Node 9) and male-headed (Node 16) were significantly more likely to cultivate in the former wetland areas than not ($CHI^2 = 116.11$; df = 10, $p < 0.05$; Cramer's V = 0.72) (**Table 5**). Among female-headed households (Node 17), there was no significant difference between those households that had or not cultivated in the former wetland areas (**Table 5**).

Beyond 2012 (Node 4), households that did not harvest papyrus for artisanal products (Node 10) were more likely to cultivate in the former wetland areas than not ($CHI^2 = 116.11$; df = 10, $p < 0.05$; Cramer's V = 0.72) (**Table 5**). In relation to whether there were restrictions on wetland utilization, households that did not know or agreed that there were restrictions (**Figure 5**), were significantly less likely to cultivate in the former wetland areas ($CHI^2 = 116.11$; df = 10, $p < 0.05$; Cramer's V = 0.72) (**Table 5**) as illustrated in the decision route of node 0, 5, and 14.

Interlinkages Between Perceptions and Wetland Use

From the CHAID analysis, perceptions on wetlands value did not influence wetland conversion to agriculture. However, investigating the interlinkages between the perceptions and the actual use of the Anyiko wetland, households that neither derived provisioning ESS from the wetland nor cultivated in the former wetland areas (32 households), were more likely to view the wetland as a "wasteland." Contrarily, households that exclusively derived provisioning ESS such as papyrus mats and fiber, palm baskets and hats, pasture, and water for livestock and aquaculture, were less likely to agree ($CHI^2 = 17.35$; df = 6, $p = 0.008$; Cramer's V = 0.196) (**Table 6**). The households that exclusively derived provisioning ESS from the wetland were also more likely to disagree that conversion of the wetland to agriculture had a higher net monetary benefit than when conserved and used for artisanal products among other provisioning ESS ($CHI^2 = 11.111$; df = 6, $p < 0.05$; Cramer's V = 0.157) (**Table 7**).

DISCUSSION

Land Use/Cover Change in the Anyiko Wetland

Agricultural expansion through drainage of wetlands has led to loss or reduction of wetland's areal coverage globally (Zedler and Kercher, 2005). The demand for wetland provisioning ESS particularly crops correlates with land use change and is one of the most pressing challenge for many African wetlands (Rebelo et al., 2010). The Anyiko wetland reduced by 55%, from 390 to 174 acres, between 1966 and 2018 (**Table 2**), of which 43% was converted to farmland (**Table 3**). In the same period, the wetland/close shrubland was completely converted to farmland. Loss of wetlands to agriculture in sub-Saharan Africa have also been reported by other studies. For example, Isunju and Kemp (2016) reported 62% of the wetland vegetation loss in Nakivubo

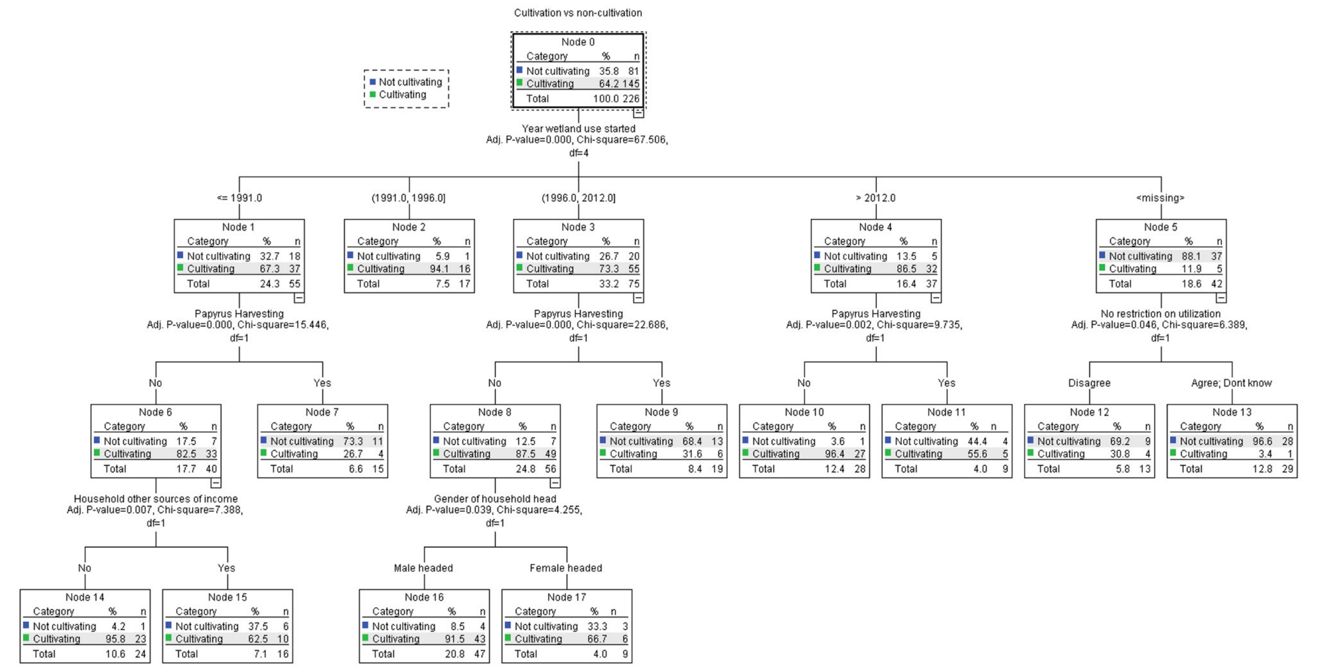

FIGURE 5 | Decision tree analysis on determinants influencing wetland utilization for agriculture.

wetland in Uganda, between 2002 and 2014, 30% of which was due to drainage and conversions to farmland. In addition, Troy et al. (2007) reported 52% loss of Ga-Mampa wetland in South Africa between 1996 and 2004 to farmland. Elsewhere, for instance, China, Zhang et al. (2010) reported ∼67% loss of wetlands in Sanjiang Plain between 1975 and 2004 due to agricultural land use.

The reduction in size of the Anyiko wetland was, however, not only because of farmland expansion, but also encroachment of open and close shrublands by 15 and 2%, respectively. This finding is consistent with the study of Isunju and Kemp (2016), which reported a loss of Nakivubo wetland in Uganda by 2% between 2002 and 2014 because of encroachment by trees and shrubs (shrubland). Typically, wetlands are inhabited by flood tolerant vegetation (Cronk and Fennessy, 2016) and therefore encroachment by shrubland indicate drying out of some parts of the wetland. This is usually initiated by human activities such as hydrological alterations through water channelization and drainages for farmland to allow crop production. The Anyiko wetland is used for rice and vegetable irrigation, whereby water is diverted from the wetland via canals and conveyed to cultivated land for irrigation. Moreover, several small canals are dug out within and around the wetland to increase water conveyance downstream. Reduced river discharge due to upstream diversions or abstraction for irrigation and conversions to agricultural land, which often includes removal of wetland vegetation and hydrological changes through channelization and drainage are noted by Osumba et al. (2010) and Owino and Ryan (2007) to be the main drivers of wetland loss in Kenyan wetlands. Hydrological connectivity between the wetland and the river (water bodies) is not only important for water supply to the ecosystem, but also nutrients and sediments, which are essential for growth of wetland vegetation and functioning of these systems (Lake et al., 2006; Khisa et al., 2013). Hence, prolonged limited lateral connectivity may result in substantial ecosystem loss (Boulton, 2003; Zhang et al., 2010).

Studies such as Van Dam et al. (2013) have reported existence of connection between flooding and conversion of wetlands to farmland in the Nyando wetland in Kenya. Flood recession agriculture is usually practiced in wetlands during the dry season, whereby the vegetation is partially cleared (no removal of below ground biomass) and crops planted. During the drier years, larger parts of the wetland are converted to farmland. Without structural changes to hydrology and removal of rhizomes, the papyrus vegetation re-grows when re-flooded. In the Anyiko wetland, the rhizomes are removed, and hydrology is altered resulting in no re-growth of papyrus and reduction of vegetated wetland area. Regrowth of papyrus (seed-based re-generation) in the wetland is, however, possible if hydrology is restored when the seed propagules are still viable (Boar, 2006).

The increase of the Anyiko wetland by 2% in open shrubland by 2018 may have been influenced by flooding of the downstream Nzoia river. Usually during a typical long rainy season (March to early June), the Nzoia river overtops its banks resulting in flooding of some parts of the wetland downstream, adjacent shrublands and farmlands, which may last up to July. Increase in riverine water levels result into flooding landward that can change dry land into a wetland (Ongwenyi et al., 1993; Kiwango

TABLE 5 | Decision routes for determination of wetland conversion to agriculture.

Terminal nodes		Not cultivating	Cultivating	Total
2: 0/2	Count	1	16	17
	Adjusted residual	−2.7	+2.7	
7: 0/1/7	Count	11	4	15
	Adjusted residual	**+3.1**	**−3.1**	
9: 0/3/9	Count	13	6	19
	Adjusted residual	**+3.1**	**−3.1**	
10: 0/4/10	Count	1	27	28
	Adjusted residual	**−3.8**	**+3.8**	
11: 0/4/11	Count	4	5	9
	Adjusted residual	+0.5	−0.5	
12: 0/5/12	Count	9	4	13
	Adjusted residual	+2.6	−2.6	
13: 0/5/13	Count	28	1	29
	Adjusted residual	**+7.3**	**−7.3**	
14: 0/1/6/14	Count	1	23	24
	Adjusted residual	**−3.4**	**+3.4**	
15: 0/1/6/15	Count	6	10	16
	Adjusted residual	+0.1	−0.1	
16: 0/3/8/16	Count	4	43	47
	Adjusted residual	**−4.4**	**+4.4**	
17: 0/3/8/17	Count	3	6	9
	Adjusted residual	−0.2	+0.2	
	Total	81	145	226

If adjusted residual is $> u\alpha = 0.05 = 3.052$ (after Boferroni correction to control for Type I error rate), the corresponding cell frequency (count) is statistically significant. + (plus) adjusted residual means more likely and – (minus), less likely.
The bold values are statistically significant adjusted residuals.

TABLE 6 | Association between the perception wetland is "wasteland" and use of the wetland.

			Wetland is a "wasteland"			Total
			Agree	Don't know	Disagree	
Wetland use	Agriculture	Count	22	5	25	52
		Adjusted Residual	−1.0	0.2	0.9	
	Wetland provisioning ESS	Count	17	7	25	49
		Adjusted Residual	**−2.2**	1.5	1.4	
	Both agriculture and wetland provisioning ESS	Count	46	6	41	93
		Adjusted Residual	0.2	−1.1	0.4	
	None	Count	25	2	5	32
		Adjusted Residual	**3.6**	−0.6	**−3.3**	
Total		Count	110	20	96	226

If adjusted residual is $> u\alpha = 0.05 = 1.96$, the corresponding cell frequency (count) is statistically significant. + (plus) adjusted residual means more likely and – (minus), less likely.
The bold values are statistically significant adjusted residuals.

and Wolanski, 2008). For instance, Khisa et al. (2013) reported wetland increase of 68% between 1950 and 1973 in the Nyando wetland in Kenya due to the periodic flood events experienced in the Lake Victoria region from 1961 to 1964. The study also reported decline of 40% between 1973 and 1986, 24% from 1986 to 2001, and 7% from 2001 to 2008 in the Nyando wetland, because of human induced hydrological alterations of the wetland leading to land cover conversions. In addition, drought in the early 1980s limited lateral connectivity between the River Nyando and the wetland and hence, contributed to the wetland loss. Therefore, change in land use/cover in wetlands may be caused by both natural (rainfall variability) and human induced hydrological alterations in the landscape. Climate change is also expected to contribute to wetland loss through hydrological alterations due to drought and changing rainfall patterns (Junk et al., 2013). Hence, climate change in combination with human induced hydrological alterations and conversion to agriculture, may further exacerbate the loss of Anyiko wetland.

Socio-Economic Determinants Influencing Wetland Utilization for Agriculture

Wetlands are more valuable than often perceived by many communities living around them (Schuyt, 2005). Stakeholders such as government ministries, policy makers and smallholder farmers frequently perceive drainage and conversion of wetlands to agriculture and human settlement surpass the benefits of their "wise use" (Schuyt, 2005; Ramsar Convention Secretariat, 2010). In this study, the perceptions that wetland is "wasteland" did not significantly influence its utilization for agriculture. The perception that conversion to agriculture had higher net monetary benefit than papyrus artisanal products among other provisioning ESS also did not significantly influence wetland utilization for agriculture. These indicates that conversion of the wetland to agriculture was not driven by these perceptions. Investigating the interlinkages between the perceptions and the actual use of the wetland, however, showed that the households which neither derived provisioning ESS from the wetland nor cultivated in former wetland areas were more likely to perceive the wetland as a "wasteland." This perception was contrary to the households that exclusively derived provisioning ESS from the wetland, indicating that action molds perceptions (Jaswal, 2016). Perception-action link is considered relatively automatic, yet action also influences what is perceived (Vernon et al., 2015). Action provides opportunities for social learning and sharing of knowledge and experience among stakeholders which influences their perception. Changes in perception influences the behavioral patterns of the stakeholders to create actions (Kitolelei and Sato, 2016). Therefore, households exclusively deriving provisioning ESS from the wetland had experienced the importance of the wetland to their livelihoods particularly through cash income from the sale of papyrus artisanal products. This suggests that the perception that Anyiko wetland is "wasteland" by households that neither derived provisioning ESS nor cultivated in the former wetland areas was motivated by

TABLE 7 | Association between the perception that agriculture has higher net monetary benefit than wetland provisioning ESS and use of the wetland.

			Higher net monetary benefit in wetland areas converted to agriculture			Total
			Agree	Don't know	Disagree	
Wetland use	Agriculture	Count	30	12	10	52
		Adjusted residual	−0.3	1.1	−0.6	
	Wetland provisioning ESS	Count	23	8	18	49
		Adjusted residual	**−2.1**	−.4	**2.8**	
	Both agriculture and wetland provisioning ESS	Count	58	18	17	93
		Adjusted residual	0.7	0.4	−1.2	
	None	Count	24	3	5	32
		Adjusted Residual	1.9	−1.4	−1.0	
Total		Count	135	41	50	226

If adjusted residual is > $u\alpha = 0.05 = 1.96$, the corresponding cell frequency (count) is statistically significant. + (plus) adjusted residual means more likely and – (minus), less likely. The bold values are statistically significant adjusted residuals.

lack of economic gain from the wetland. The term "wasteland" therefore may have more underlying economic motivation than resulting from a traditional view as noted by Maltby (2013, p. 9). The economic gain may have also influenced households exclusively deriving provisioning ESS from the wetland that conversion to agricultural use did not have higher net monetary benefit. The households acknowledged higher cost of production for crops like rice as the basis for their view. Since perception action link is interdependent, it is expected that the perceptions of households exclusively deriving provisioning ESS influenced the households not to cultivate in the former wetland areas. Alternative sources of income, however had a significant influence on Anyiko wetland conversion to agriculture as shown in the CHAID analysis.

Households that started using the wetland before 1991, did not harvest papyrus for artisanal products and lacked alternative sources of income, were more likely to utilize the wetland for agriculture than not. This implied that conversion of the Anyiko wetland to agriculture for these households may be driven partly by the need to generate income. Crops grown in the wetland such as rice, collard greens, sugarcane, and coco yams are majorly for sale and therefore, generates income for the households. This supports Wood and van Halsema (2008) argument that partial or full conversion of wetlands for agriculture may be economically and financially motivated. The finding of the study is consistent with Turyahabwe et al. (2013) who report on wetlands in Kyoga plains agro-ecological zones in Uganda, where growing crops in wetlands is more dominant within households with limited sources of income. Kangalawe and Liwenga (2005) also reported crop production in wetlands as the main source of income in Kilombero Valley wetlands in Tanzania. The crops grown in the former wetland areas of the Anyiko wetland were also used for subsistence purposes and hence supplemented crop production from upland farms. Lack of alternative livelihood opportunities, however, is noted by Rebelo et al. (2010) to hinder prevention of wetland conversion to agriculture. Therefore, in the Anyiko wetland, if provision of alternative sources of income is not addressed in future, there is a likelihood of continuous conversion to agriculture to generate income.

Households harvesting papyrus for fiber and mats production were less likely to engage in wetland cultivation than not. This may be attributed to the labor intensive nature of production of papyrus artisanal products. For instance, households harvesting papyrus for mats production spend ∼5 days in a week harvesting papyrus for 3 h (including splitting of culms and their transportation home when dry) and use 4 days a week and 4 h to make the mats at home. Farming in the former wetland areas is also labor intensive e.g., canal digging to minimize farm flooding and for rice and vegetables irrigation, bird scaring for rice farmers, farm expansions through wetland drainage and vegetation clearing etc. This implies that households may not be able to engage in both farming and papyrus harvesting for artisanal products due to the labor intensive nature of both livelihood activities. Harvesting of papyrus for artisanal products also serve as alternative source of income because products such as papyrus mats and fiber are mainly used for sale. This suggests that, apart from wetland cultivation and papyrus harvesting for artisanal products being labor intensive, these households had alternative source of income (papyrus products) unlike households that were not harvesting papyrus.

In such a case, whereby both farming and harvesting of papyrus is labor intensive, household size (with assumption of age, availability, and fitness) plays a significant role in provision of labor force. According to Taruvinga and Mushunje (2010) larger household sizes have benefits of labor force in wetland utilization. In addition, large household size has higher food consumption burden and greater dependence on wetlands not only for crop production, but also other provisioning ESS than small household size. In this study, however, household size did not significantly influence wetland utilization for agriculture. The average household size for wetland cultivating (5 ± 2 people) and non-cultivating (4 ± 2 people) households were not significantly different. Contrarily, using binary logistic regression, Taruvinga and Mushunje (2010) reported that household size had a significant influence on participation in wetland cultivation in Mashonaland East Province of Zimbabwe whereby larger household sizes were less likely to cultivate in the wetland than smaller household sizes. Zidana et al. (2007) also reported that household size significantly influenced cultivation of Lilongwe and Linthipe river banks in Malawi as larger household sizes were more likely to cultivate in the river banks than smaller household sizes.

In this study, male-headed households that were not harvesting papyrus were significantly more likely to cultivate in the wetland than not. This suggests that the limited alternative sources of income may have contributed to male-headed households to participate in wetland cultivation. Chinsinga (2007) points outs that wetland cultivation is predominantly feminine activity when other lucrative alternatives are available. Taruvinga and Mushunje (2010), however, reported no significant effect of gender of household head on wetland cultivation in Mashonaland East Province of Zimbabwe.

Households that either agreed or did not know that there were restrictions on wetland utilization were significantly less likely to cultivate in the wetland. Usually, wetlands are one resource with many interests and do not have clear property rights (Schuyt, 2005). This makes them prone to over-exploitation, degradation, and conversion to agriculture due to conflicting uses by stakeholders. In the Anyiko wetland, there are not any restrictions on deriving provisioning ESS from the wetland e.g., harvesting papyrus for artisanal products, grazing livestock, or withdrawing water for irrigation. However, cultivation in the wetland is restricted by households whose upland farms are adjacent to the wetland or had reclaimed some parts of the wetland for agriculture in the earlier years. Therefore, other households which do not own cropland in the former wetland areas may only grow crops in the converted areas or reclaim more of the wetland for agriculture, if leased out to them at a fee. This implied that the households could still hire wetland plots from the owners at a fee. Therefore, it may suggest that other factors other than restriction on cultivation hindering them from farming in the wetland. Unlike this study, in other findings in sub-Saharan Africa e.g., Adekola et al. (2012), Taruvinga and Mushunje (2010), and Rebelo et al. (2010), village heads/council were responsible for allocation of wetland plots for farming and putting of regulations e.g., size of plot per household among others.

Predictors such as age of the respondent and their highest formal education level, household annual alternative income amount and household location (village) did not have a significant effect on wetland utilization for agriculture. The average age of the respondent whose households were cultivating (49 ± 17 years) in the former wetland areas and those not cultivating (52 ± 17 years), were not significantly different and hence, may not have influenced whether a household utilized the wetland for agriculture. Study by Taruvinga and Mushunje (2010) though did not compare the age of cultivating and non-cultivating households, showed that the likelihood of wetland cultivation increased with increasing age of the household head. In relation to formal education, majority of the respondents, both from cultivating and non-cultivating households had attained primary school as their highest formal education level or had no formal education (**Table 4**). A small proportion such as 2% for cultivating and 3% for non-cultivating households had attained college education. This suggests that access to formal employment opportunities in Kenya are limited to majority of the respondents in both cultivating and non-cultivating households. Therefore, the low literacy level among the respondents may be an impediment to the households' access to alternative sources of income. Zidana et al. (2007) and Taruvinga and Mushunje (2010) reported that the more educated the household head was, the less likely were the household cultivating in the former wetland areas. Participation of less educated households on wetland cultivation was attributed to limited access to non-farming income. Kipkemboi et al. (2007) though did not categorize the households studied as wetland cultivating and non-cultivating reported that dependence of households on wetland provisioning ESS including crops in Nyando wetland in Kenya increased with increasing education level. The highest formal education level attained by most of the respondents, however, was primary and secondary level (78.5%). Average household annual alternative income amount between cultivating ($ 393 ± 1,022) and non-cultivating ($ 424 ± 1,249) households were not significantly different and hence, may have no influence on whether a household engaged on wetland utilization for agriculture. The non-significant effect of the village on wetland utilization for agriculture suggests that the wetland accessibility for cultivating and non-cultivating households was not dependent on household location. The households were not restricted to cultivate only on the wetland areas neighboring their respective villages.

Association among the variables in this study is neither correlation nor causation in all cases. Association is a general relationship: one variable provides information about another. Correlation is more specific: two variables are correlated when they show an increasing or decreasing trend (Altman and Krzywinski, 2015). Associations can arise between variables in the presence and absence of a causal relationship. Therefore, association does not imply causation while correlation implies association, but not causation. On the contrary, causation implies association, but not correlation.

Employed Methods and Limitations

Landsat satellite image and binary logistic regression are commonly used in sub-Saharan Africa for analysis of land use/cover change and determinants of wetlands utilization for agriculture, respectively. This study used panchromatic photographs and color satellite image data, and CHAID decision tree model. The studies on land use/cover change focused on relatively larger wetlands (>5 km^2) compared to Anyiko wetland (0.7 km^2) and hence, Landsat image spatial resolution were suitable for change analysis. Change analysis as well as identification of small wetlands (<5 km^2) is noted by Mwita et al. (2013) as difficult on the Landsat images because of low spatial resolution. In this study, though the spatial resolutions of the images were very high (3 and 0.5 m for 1966 and 2018 images, respectively), the mapping unit of 1 acre may limit the existence and/or loss of the wetland and other land use/cover types smaller than 1 acre. Therefore, some land/use cover types in this study may be over-estimated or underestimated. This study also collected socio-economic data at household level by conducting questionnaire survey. Factors beyond household level may influence wetland conversion to agriculture and hence, other stakeholders (e.g., policy makers, local/regional authorities) should be included in future studies.

The CHAID decision tree model illustrates multilevel (segments in the decision tree arranged in a stepwise manner from the first split to the terminal nodes) interactions among socio-economic status of the households to identify stepwise pathways to wetland conversion to agriculture. This is not achievable with a binary logistic regression. This implies that the CHAID method can detect unique interactions among the independent variables within the studied households that would have gone unnoticed using a binary logistic regression. Nevertheless, the CHAID method requires a large sample size to produce reliable analysis due to its multiway splits (Milanović and Stamenković, 2016). Hence, future studies should consider a larger sample size. In addition, since there are several socio-economic determinants of wetlands utilization for agriculture at household level, future studies should include more independent variables. This is not only important in improving the model performance, but also in examining the research question at varying perspectives.

CONCLUSION AND POLICY IMPLICATION

The substantial reduction in areal coverage of Anyiko wetland explicitly showed the spatiotemporal extents of agricultural expansion in wetlands in East Africa. Though inadequate understanding of wetlands values to stakeholders (e.g., policy makers, government, local communities etc.) has been documented as a major contributor to wetlands conversion, other socio-economic status of the households play a significant role in land use/cover change of wetlands. A CHAID decision tree analysis illustrates interactions among the socio-economic determinants including households' perceptions on the value of the Anyiko wetland in stepwise pathways. Such interactions would have gone unnoticed while conducting conventional methods like a binary logistic regression. Therefore, this study concludes that:

1. Anyiko wetland area coverage has reduced by more than a half between 1966 and 2018, majority (43%) of which is due to conversion to farmland. Encroachment of shrubland has also contributed to a substantial loss (17%) of the wetland.
2. At household level, conversion of the wetland to farmland was not driven by the perceptions that it is a "wasteland" and agriculture has higher net monetary benefit than when conserved and used for artisanal products among other provisioning ESS. Household socio-economic determinants: not harvesting papyrus for artisanal products, lack of alternative sources of income and gender of household head however significantly influenced conversion of the wetland to farmland.
3. The CHAID decision tree through recursively partitioning of variables into homogenous groups from the root to terminal nodes allows identification of the interactions among the socio-economic determinants of wetland conversion in graphical pathways, unlike logistic regression.

There is need for a more effective institutional regulatory framework that will promote a balance between competing interests of food production and wetland conservation. This can be achieved through intersectoral collaboration geared toward resource use efficiency, wetland products value addition, promotion of livelihood activities that have potential to reduce the impacts on wetland properties such as ecotourism, zonation to regulate human activities in the wetland among many other initiatives. Incentives for wetland restoration and climate change adaptation should be integrated into the county development plans. Lastly, it is important note that whereas social dynamics may correlate with the observed changes in land use, there is need to unpack the wetland-specific complex causal factors that may contribute to loss of wetlands including direct and indirect drivers and the associated pressures.

DATA AVAILABILITY STATEMENT

Socio-economic dataset generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

This study was approved by the National Commission for Science, Technology & Innovation (NACOSTI) as per the national regulations of research in Kenya. Before the start of the household survey, local authorities (chiefs and village heads) were informed of the research and once they were sufficiently briefed, they also approved the study. An informed verbal consent was obtained from the household respondents prior to conducting the questionnaire survey.

AUTHOR CONTRIBUTIONS

RO designed the study, collected and analyzed the data, and wrote the manuscript. FV gave guidance on land use/cover change analysis using CORONA and Google Earth images. NK and JK assisted in the manuscript write up. TH and EL offered statistical guidance. TH and ES offered guidance on the study design and write up of the manuscript.

FUNDING

This research has been funded by the Austrian Partnership Programme in Higher Education and Research for Development (APPEAR), a programme of the Austrian Development Cooperation (ADC), and implemented by the Austrian Agency for International Cooperation in Education and Research (OeAD-GmbH).

ACKNOWLEDGMENTS

The authors are indebted to Limnology and Wetland Management Programme (LWM) Egerton University and University of Natural Resources and Life Sciences Vienna (BOKU) and Doctoral School Human River Systems in the 21st Century (HR21) at BOKU for support (hr21.boku.ac.at). We are also grateful to Dr. Daniel Kyalo of Kenyatta University in Kenya for guidance on the questionnaire formulation, Zephaniah Ajode and Erick Owino for field assistance. Chief of North East Ugenya Location and assistant chiefs of Ramunde, Sihayi and Jera sub-locations for their support.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2019.00207/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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in Environmental Science

ORIGINAL RESEARCH
published: 25 March 2020
doi: 10.3389/fenvs.2020.00029

Detecting Native Freshwater Fishes Using Novel Non-invasive Methods

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Improving the ability to detect and quantify rare freshwater fishes in remote locations is of growing conservation concern, as the distributions of many native fishes are contracting to such locations where there are reduced anthropogenic and invasive species pressures. However, conventional sampling methods, e.g., backpack electrofishing and seines, tend to be heavy and bulky, thereby making them difficult to transport into remote areas with no road access. These conventional sampling methods also require physical handling of fishes, which may cause stress, harm, and mortality–all undesirable side effects for rare fishes. Thus, visual observation methods, such as underwater camera and snorkel surveys, and environmental DNA (eDNA), that are easily transportable and do not require physical handling of fishes, are being more frequently used in freshwater ecosystems. However, there have been few studies on the relative effectiveness of these three methods for detecting and quantifying freshwater fishes. In this study, the species-specific detection probabilities between the three methods, and abundance estimates derived from the visual observation methods were compared, and their utility for sampling rare fishes in remote locations in South Africa was evaluated. Underwater cameras and snorkel surveys detected slightly different species within a fish community. For the redfins, the detection probability using underwater cameras (0.96, SD = 0.03) was highest, followed by snorkel surveys (0.93, SD = 0.05), and eDNA (0.70, SD = 0.21). The visual observation methods were positively correlated with pool length, while eDNA was negatively correlated with turbidity. For Cape Kurper, the detection probability using underwater cameras (0.75, SD = 0.15) was highest, followed by snorkel surveys (0.68, SD = 0.16), and eDNA (0.64, SD = 0.19); all three methods were negatively affected by water turbidity. It is recommended that decisions on which sampling method to use in remote locations should depend on whether the study requires population- or community-level information, spatial scale required, and resource availability, as each method has its own strengths and weaknesses. Generally, eDNA is the most expensive method and requires specialized facilities and equipment, while underwater cameras require video analyses that are more time consuming to analyze than snorkel surveys.

Keywords: underwater cameras, snorkel surveys, eDNA, streams, endangered fishes, South Africa, detection probability

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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *15 December 2019*
Accepted: *28 February 2020*
Published: *25 March 2020*

Citation:
Castañeda RA, Van Nynatten A, Crookes S, Ellender BR, Heath DD, MacIsaac HJ, Mandrak NE and Weyl OLF (2020) Detecting Native Freshwater Fishes Using Novel Non-invasive Methods. Front. Environ. Sci. 8:29. doi: 10.3389/fenvs.2020.00029

INTRODUCTION

Imperfect detection of species biases our ability to quantify community richness and population abundances (Guillera-Arroita, 2017). The magnitude of this imperfect detection varies based on the rarity and behavior of a species, while our ability to detect the species will vary based on sampling methods (MacKenzie et al., 2018). This is further complicated when the focal species are endangered as most conventional sampling methods require capture and physical handling of animals, inducing stress on and, at times, causing mortality of, target species and by-catch (Putman, 1995; Romero, 2004; Ellender et al., 2016). This is especially true when sampling and monitoring freshwater fishes. For example, electrofishing can have a mortality rate of 3–10% and cause other injuries, such as spinal fractures, that would affect the fish's ability to survive (Snyder, 2003; Dolan and Miranda, 2004). A 3% mortality rate may be acceptable for widely distributed fishes with large population sizes but may have a population-level effect on endangered species with restricted distribution ranges. In addition, the distributions of many endangered fishes have been contracting into headwater areas, into refuges from invasive species and other anthropogenic disturbances that have yet to reach (Lowe and Likens, 2005; Colvin et al., 2019). In many places, headwater refuges are in remote locations with little to no road access where bulky conventional sampling equipment, such as backpack electrofishers and seine nets, may be impossible to transport (Thurow et al., 2012; Ebner et al., 2015). Therefore, readily-transportable, non-harmful sampling techniques are required to offset stress and injury to endangered fishes and by-catch in remote areas (Costello et al., 2016). In freshwater systems, visual observation and environmental DNA (eDNA) are increasingly popular non-invasive sampling methods (Janosik and Johnston, 2015; Struthers et al., 2015). Visual observation techniques can be undertaken using underwater cameras or snorkeling (Ellender et al., 2012; Struthers et al., 2015) and eDNA tests for the DNA of organisms in water samples to assess species presence (Lacoursière-Roussel et al., 2016a).

Underwater camera recordings are frequently used in freshwater and marine ecosystems (e.g., Struthers et al., 2015; King et al., 2018; Castañeda et al., 2020); this method has many advantages and some disadvantages (Mallet and Pelletier, 2014). Underwater cameras can be used to estimate relative abundance and species richness and study the behavior of fishes in their natural environment but require clear water to do so. Recordings can be stored and verified by other investigators. However, cameras require accessories for power and memory (Friesen and Chivers, 2006; Thurow et al., 2012; Assis et al., 2013; Ebner and Morgan, 2013; Domenici et al., 2014; Mallet and Pelletier, 2014; Struthers et al., 2015). If electricity is not accessible, as in many remote areas, extra batteries or alternate power sources (e.g., generators, solar panels) and memory cards are required. These specialized electronics may be expensive or unfeasible to purchase for some researchers working in remote areas; hence, snorkeling surveys may be better suited in these situations.

Snorkeling is another visual observation method that has been used to detect and estimate fish densities in small headwater streams (Weyl et al., 2013; Chamberland et al., 2014; Ellender et al., 2018). Snorkel surveys generally outperform seining and electrofishing, except when sampling cryptic species (Brock, 1982; Jordan et al., 2008; Saunders et al., 2011). Generally, snorkel surveys tend to be the most simple and cost-efficient method for observing fishes, as it requires very little equipment. Information on community composition, population size structure, and habitat use can be collected using snorkel surveys (Thurow and Schill, 1996; Ebner et al., 2015; Macnaughton et al., 2015). However, snorkel surveys could be limited by water depth, water clarity, and snorkeler training and experience, factors that could reduce consistency in, and reproducibility of, the data collected (Thurow et al., 2012). In marine environments, there has been much debate as to whether underwater cameras or snorkel surveys collect the most accurate and precise data on fish populations and communities (Langlois et al., 2010; Pelletier et al., 2010; Watson et al., 2010); however, comparative studies between the two visual observation methods are rare in freshwater habitats (Ebner et al., 2015). Although underwater cameras and snorkel surveys are becoming more widely used in freshwater ecology, we know little about the relative efficiencies of detecting rare fishes.

Environmental DNA is an increasingly used non-invasive method for surveilling invasive and endangered fishes in freshwater ecosystems. eDNA protocols concentrate DNA molecules that have been shed into their local environment (e.g., water, soil, snow, air) to detectable levels using PCR (Ficetola et al., 2008; Thomsen and Willerslev, 2015). PCR-based assays may target individual species with high specificity (Baker et al., 2018; Fernández et al., 2018; Mauvisseau et al., 2019), or facilitate the holistic screening of entire biotic communities through the massively parallel DNA sequencing of diagnostic genetic markers (Harper et al., 2018), and have made it possible to detect DNA from water samples even at very low quantities (Ficetola et al., 2008; Thomsen and Willerslev, 2015; Harper et al., 2018). However, the high sensitivity of eDNA increases the risk of false positives from contamination, requiring specialized tools for collecting water samples in the field and a clean laboratory set up for extracting DNA separate from the PCR/sequencing facility (Goldberg et al., 2016). Despite these costly hurdles, the economies of scale associated with a high-throughput method like eDNA has led to its application in many large-scale monitoring projects (Jerde et al., 2013; Biggs et al., 2015; Balasingham et al., 2018). However, the effectiveness of eDNA studies may depend on the hydrological and physical aspects of the habitat (Jane et al., 2015; Balasingham et al., 2017; Harper et al., 2018), and species-specific differences in shedding, behavior, and abundance (Thomsen and Willerslev, 2015). In addition, eDNA studies have predominantly focused on temperate species, and the utility of these studies in warmer tropical and subtropical conditions may differ (Eichmiller et al., 2016; Cantera et al., 2019; Doble et al., 2019).

The purpose of this study is to compare the detection probabilities and abundance estimates of the two visual observation methods and eDNA for fish communities in remote locations and to assess which method is best suited in different situations. The study focuses on the Eastern Cape

Redfin (*Pseudobarbus afer*), Gamtoos River Redfin (*Pseudobarbus swartzi*), and Cape Kurper (*Sandelia capensis*) in a remote area of Eastern Cape Province of South Africa. Eastern Cape Redfin is listed as Endangered by IUCN (Chakona et al., 2017a), the closely related Gamtoos River Redfin is listed as Vulnerable by IUCN (Chakona et al., 2017b), and Cape Kurper is Data Deficient but has a declining population trend (Chakona, 2018). We hypothesize that the detection probabilities of all three methods will decrease with increasing spatial scale of the pools sampled within the streams (length, width, depth) and with increasing water turbidity.

MATERIALS AND METHODS

Study System

The study was conducted in four clear headwater streams in Eastern Cape Province, South Africa typical of headwater stream refugia for native fishes in the eastern part of the Cape Fold Ecoregion (Ellender et al., 2017). Three streams, Fernkloof, Waterkloof, Blindekloof, tributaries to the Swartkops River, are within the Groendal Wilderness Area (**Figure 1A**) and the Bos River tributary of the Kouga River which runs in part through the Skilderkrantz Private Nature Reserve (**Figure 1B**). Both the Skilderkrantz Private Nature Reserve and the Groendal Wilderness Area are within the Baviaanskloof Mega Reserve and are part of the Cape Floral Region Protected Areas World Heritage Site (UNESCO, 2015). The tributaries run through mountainous areas, bounded by indigenous forest, with few roads or maintained trails to provide access to them. Reaching the sampling sites requires hours of hiking through rugged terrain and wading and swimming through pools (**Figure 2**). Both watersheds have low native freshwater fish species richness (Ellender et al., 2017). Fish faunas contain African Longfin Eel (*Anguilla mossambica*), Cape Kurper, Goldie Barb (*Enteromius pallidus*), and River Goby (*Glossogobius callidus*), Eastern Cape Redfin and Gamtoos River Redfin (**Supplementary Table 1**) (Chakona and Skelton, 2017; Ellender et al., 2017). Both watersheds have had intentional and unintentional introduction and establishment of non-native fishes. Non-native faunas include Common Carp (*Cyprinus carpio*), African Sharptooth Catfish (*Clarias gariepinus*), Largemouth Bass (*Micropterus salmoides*), Smallmouth Bass (*Micropterus dolomieu*), Spotted Bass (*Micropterus punctulatus*), and Banded Tilapia (*Tilapia sparmanii*) (**Supplementary Table 1**) (Ellender et al., 2011). Because Eastern Cape Redfin and Gamtoos River Redfin were, until recently (Chakona and Skelton, 2017), considered the same species within the *Pseudobarbus afer* complex throughout the sampling period and exhibit very similar ecologies, the data from the two species were combined in the study and termed redfins.

Data Collection

In February and March 2015, sampling for freshwater fishes using cameras, snorkel, and eDNA snorkel surveys was conducted in isolated pools along the length of the streams. For cameras and snorkel surveys, 23 pools were sampled spanning 8 km in the Bos River, 4 pools spanning 3 km in the Kouga River, 13 pools spanning 3 km in the Fernkloof, 10 pools spanning 3 km in the Waterkloof, and 19 pools spanning 5 km in the Blindekloof (**Figure 1**). For eDNA, water samples were taken at seven sites in the Bos River, three sites in the Kouga, four sites in the Fernkloof,

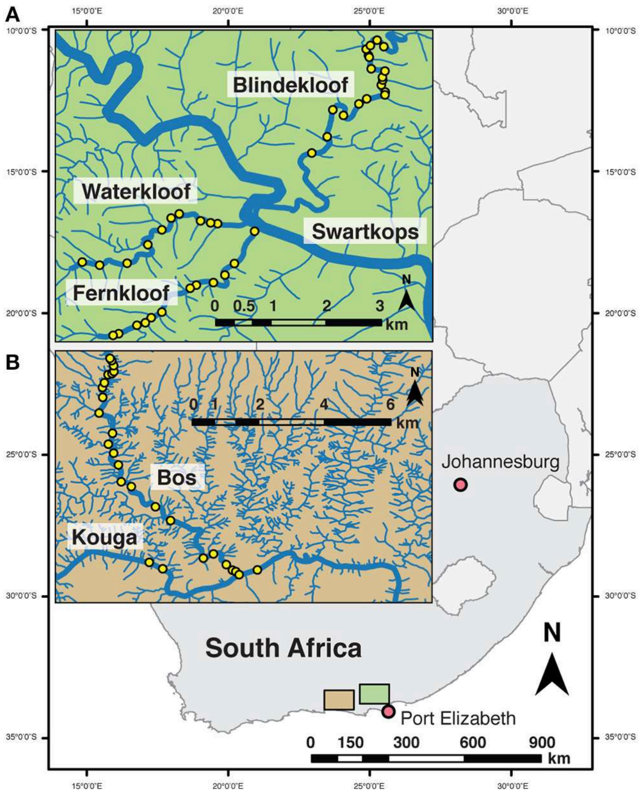

FIGURE 1 | Location of sampling sites (yellow points) across two watersheds in Eastern Cape, South Africa; **(A)** Swartkops watershed within the Groendal Nature Reserve; and **(B)** Kouga watershed, Bos River tributary within the Skilderkrantz Nature Reserve.

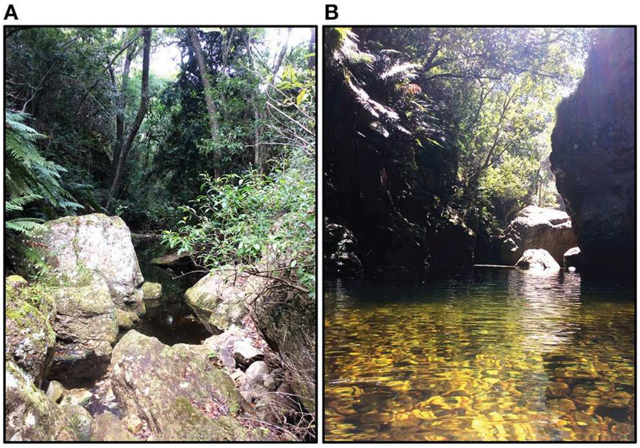

FIGURE 2 | Headwater tributaries in the Swartkops River watershed. Example of: **(A)** no trail through the rugged terrain and thick forest typical across sites; **(B)** steep overhanging cliffs framing the tributary requiring wading and swimming across the pool to access upstream sites.

four sites in the Waterkloof, and four sites in the Blindekloof, which were all a minimum of 500 m apart.

Water samples for eDNA analysis were taken before any field personnel waded through the stream and before deploying other sampling gear to prevent contamination from field clothing and equipment that had been in contact with stream water downstream. Three 2-L water samples were taken within 5 cm of the surface of each pool using pre-sterilized Nalgene polycarbonate plastic collection bottles. Sterilization of the collection bottles and carrying dry-bags was done at the field station before sampling by soaking them in a 10% bleach solution (of 6% w/v sodium hypochlorite) for at least 10 min, then air dried. All collected water samples were packed in ice and after three or four pools were sampled, they were carried immediately downstream to the field station for filtration. All eDNA water samples were collected in <5 field days.

Upon returning from the sampling area, water samples were filtered on the same day at the field station in a room dedicated to filtration that was cool and sterilized. A vacuum pump and tripartite manifold filtration system were used to filter the water samples through glass microfiber filter papers [47 mm diameter, 1.2 μm pore size (VWR 696-filter, product No: 28333-139)]. Sterile forceps were used to manipulate the filter papers onto the funnels and into microcentrifuge tubes. Approximately half of the water was processed per filter paper resulting in two filter papers per water sample, which were stored in separate microcentrifuge tubes and filled with molecular grade ethanol (> 95%). The process was repeated for each water sample where all equipment was sterilized and dried between samples. Controls were conducted using the same procedure with distilled water between sample runs.

eDNA samples and the environmental controls were extracted in a UV cabinet in a building separate from the facility used for PCR using a modified DNeasy Blood & Tissue Kit (Qiagen) protocol designed for eDNA samples (Goldberg et al., 2011; Lacoursière-Roussel et al., 2016b). DNA concentrations were taken for a subset of the eDNA samples, environmental controls, and extraction controls using a Qubit 4 Fluorometer (Invitrogen) to ensure extraction success.

Forward and reverse primers were designed to target a < 200 bp region of the *cytochrome b* mitochondrial gene of both redfins (*P. afer* and *P. swartzi*) and Cape Kurper (*S. capensis*) ensuring at least 6 nucleotides differ between the target species and other co-occurring species in the localities sampled (**Supplementary Table 1**). The specificity of these primers (**Supplementary Table 2**) for solely the target species was tested *in vitro* using conventional PCR with genomic DNA from each target species and other co-occurring species as the template. Genomic DNA was extracted from tissue samples preserved in ethanol extracted using a DNeasy Blood & Tissue Kit (Qiagen). Each PCR reaction contained 6 μL of 2X Phusion Hot Start II High-Fidelity DNA Polymerase, 600 nM of forward and reverse primers, 2 μL of template DNA, and ddH_2O for a final volume of 12 μL. Following an initial denaturation phase at 95°C for 3 min, DNA was amplified for 40 cycles of 98°C (20 s), 60°C (15 s), and 72°C (15 s), followed by a 5 min extension phase at 72°C. PCR products were visualized on a 2% agarose gel and were compared to an 100 bp ladder to check that amplicons were the correct size. At least one amplicon from each watershed was purified and sequenced using Sanger sequencing to further ensure the specificity of each primer pair.

All eDNA samples, environmental controls, and extraction controls were tested for the presence of redfins and Cape Kurper using quantitative PCR (qPCR). Each qPCR reaction contained 10 μL of Power SYBR Green Master mix (Applied Biosystems), 200 nM of the species-specific forward and reverse primers (**Supplementary Table 2**), 4 μL of template (diluted in ddH_2O 1:10), and ddH_2O for a final volume of 20 μL. Each sample was assayed in triplicate on a 96 well plate alongside at least three no template controls (NTCs) containing ddH_2O instead of template. All plates were analyzed on a QuantStudio^{TM} 3 Real-Time PCR System (Applied Biosystems). Thermocycler conditions were set to the manufacture's defaults (50°C for 2 min; 95°C for 2 min; followed by 40 cycles of a 15 s 95°C denaturation step and an annealing/extension step of 1 min at 60°C). Cq values, a measure of when the fluorescent signal passes the threshold for detection, were calculated using the second derivative method. Amplification of the correct target sequence and absence of primer-dimers was confirmed by a comparison of a melt-curve assay (from 60 to 95°C). Positive sequence identity of the qPCR products was also confirmed with a BLAST search of the Genbank nucleotide database with query sequences from a subset of PCR products sequenced at the TCAG sequencing facility at the Hospital for Sick Children, Toronto. The limit of detection (LOD) and the efficiency of the qPCR reaction was determined using a standard curve, as MIQE guidelines [Minimum Information for the Publication of Quantitative PCR Experiments (Bustin et al., 2009)], generated using 10-fold dilutions of genomic DNA from 1 to 1×10^{-6} ng/μL for *P. swartzi* and 10 to 1×10^{-6} ng/μL for *S. capensis*. A positive hit for each target species in the eDNA and control samples was assigned to a sampling site if the fluorescent signal of any of the three technical replicates surpassed the threshold for detection and if melt temperatures were within the range of temperatures observed in analysis of genomic DNA samples (78–79°C for the *S. capensis* and 75–76°C for *P. swartzi*). We removed any eDNA samples from the analysis if any hits were detected in an environmental control taken from the same site.

After collecting eDNA samples, a GoPRO (Hero4 Black) was mounted on a flexible tripod (GorillaPod) and placed at the end of each pool facing upstream. The camera recorded video for 30 min (video resolution 1080p, 30 frames per second, ultra-wide frame of view, and 1,920 × 1,080 screen resolution) (Ellender et al., 2012). A 30 min recording is standard for monitoring native fish populations in South African streams and rivers and is sufficient to achieve the highest MaxN (Ellender et al., 2012; Weyl et al., 2013). In the lab, all videos were viewed, and the maximum number of adult and juvenile fishes was recorded for every 30 s time frame and scored as a positive detection. MaxN was used as the measure of relative abundance (Campbell et al., 2015), in which the single highest count of a target in the specific recording is retained.

Upon retrieval of the camera, a two-pass snorkel survey was conducted where the snorkeler started at the downstream end of the pool and zigzagged upstream (to maximize sampling all microhabitats across a pool) until they reached the end of the pool and repeated the same zigzagging pattern back downstream (Ellender et al., 2011). All fishes observed were identified to species and counted. The counts of the two passes were averaged and converted to density (fish m^{-2}), by dividing the average count by the surface area [length (m) × average width (m)] of the sampled site (Ellender et al., 2012; Weyl et al., 2013).

At each pool, several habitat variables, hypothesized to affect the occupancy of the fishes and detection probability of the different gear types, were measured. Total length (m) of the pool was measured; then the pool was separated in 5–6 transects of equal length, and the width (m) of each transect measured. At each transect, depth (m) and the dominant sediment type, was recorded at 0.2 m from the waterline on each side and at the midpoint of the stream, totaling three sampling points per transect (Ellender et al., 2012). Water turbidity (nephelometric turbidity units–NTU) was measured using a Hanna HI 98703 turbidimeter (HANNA Instruments Inc., Woonsocket, USA).

Statistical Analysis

Multi-scale, single-season occupancy models were built to calculate the detection probabilities of each gear type for the native and non-native fishes (Nichols et al., 2008; MacKenzie et al., 2018). The multi-scale, occupancy-model approach estimates the detection probability of different gear types (p) deployed during the sampling period, probability of occupancy (ψ), and probability that the species is present during the sampling (θ) (Nichols et al., 2008). The top occupancy model was determined by holding detection probability constant and testing the different habitat covariates on occupancy; the model with the lowest AIC was used to determine detection probabilities of each gear type. Using the top occupancy model, detection probability was modeled as constant across sampling methods, different across methods, and covarying with average pool depth (m), average pool width (m), pool length (m), surface area (m^2) [length (m) × average width (m)], volume (m^3) [length (m) × average width (m) × average depth (m)], and turbidity (NTU). Correlated variables were not included in the same model. We hypothesized that an increase in any of these spatial covariates would negatively affect the detection probability of each method, as cameras and snorkelers have a limited field of view (Thurow et al., 2012), and DNA can be diluted in larger water bodies (Jane et al., 2015). Further, we hypothesized that turbidity would have a negative effect on the detection probabilities of all three methods, as an increase in turbidity would reduce visibility, a requirement for visual observation methods (Thurow et al., 2012), and turbidity, which can be a proxy for PCR inhibitors present in the water, can decrease detection by eDNA (Jane et al., 2015). For camera detections, if a fish was seen at least once in a video recording it was scored as 1; for snorkel surveys, if the fish was seen in at least one of the two passes then it was scored as 1; and, for eDNA if there was one positive hit in one of the three water samples taken then it was scored as 1. To determine if three water samples are needed per pool, the same occupancy models were re-run with the three detections, e.g., if two of the three water samples had a hit, then it was scored as 1, 1, 0. Using the program PRESENCE, models were run to calculate maximum likelihoods, and model selection was performed using AIC (Hines and MacKenzie, 2018). The model-averaged estimates were also calculated to obtain an overall detection probability for all three methods (MacKenzie et al., 2018). To assess the goodness of fit of our occupancy models, we attained the overdispersion parameter (c) by using Pearson chi-square statistics and parametric bootstrap test by running 10,000 bootstraps for the most global model (MacKenzie and Bailey, 2004). For models that were underdispersed ($c < 1$), $c = 1$ was set, and, for overdispersed models ($c > 1$), quasi-AIC (QAIC) was used, and AICc was used to correct for small sample sizes (Burnham and Anderson, 2002).

To test whether there is a correlation between the abundance estimates collected using underwater cameras and snorkel surveys, Spearman correlation tests were used due to the non-parametric nature of the abundance data. Data normality was tested using the "olsrr" package in R (Hebbali, 2018; R Core Team, 2019). Correlation tests were run between underwater camera MaxN and snorkel averaged count data, and underwater camera MaxN and snorkel density (individuals m^{-2}) (Ellender et al., 2012; R Core Team, 2019). To run linear regressions, the abundance data were $\log_{10}(x + 1)$ transformed to normalize the distribution of the residuals. To investigate the variation in habitat characteristics of the pools and fish densities between the tributaries, a Kruskal-Wallis test followed by Dunn's *post-hoc* test was used (Dinno, 2017).

RESULTS

Fish Community Detection and Species-Specific Detection Probabilities Vary Between Methods

The species-specific qPCR primers designed for this study were specific for the target species and had good efficiency scores (102%) with a LOD of 1×10^{-4} ng/μL for *P. swartzi* and 1×10^{-5} ng/μL for *S. capensis* (**Supplementary Figure 1**). The eDNA analysis detected *Pseudobarbus* spp. in 14 of 22 sampling sites and *S. capensis* in 10 of 22 sites and was generally consistent across technical and biological replicates (**Supplementary Table 3**).

The raw detection data revealed that the visual observation methods detected most of the fish species, although there were slight, but not significant, differences between methods. Generally, underwater cameras slightly outperformed snorkel surveys for all fish species except for Goldie Barb and River Goby (**Table 1**). The cameras detected Goldie Barb 75% of the time while snorkel surveys detected it 81% of the time, and River Goby was detected by these methods 82 and 100% of time, respectively. These percentages are overestimates of detection as we cannot confirm that a species was present in a pool if it was not detected by either visual observation method, i.e., imperfect detection was not being considered as there were too few encounters to run the occupancy models. Underwater camera was the only method that detected African Longfin Eel and African Sharptooth Catfish.

Estimating the detection probabilities of the three methods was done only for redfins and Cape Kurper as there was

TABLE 1 | Number of detections of each fish species by underwater cameras (cam) and snorkel surveys (snork), and eDNA across sampled sites.

Species	Total of 69 sites sampled			Total of 22 sites sampled			
	cam	**snork**	**Pools with fish presence**	**cam**	**snork**	**eDNA**	**Pools with fish presence**
Redfins (*Pseudobarbus afer*, *Pseudobarbus swartzi*)	50	48	51	16	16	14	16
Goldie barb (*Enteromius pallidus*)	12	13	16	–	–	–	–
Cape kurper (*Sandelia capensis*)	34	32	36	10	10	10	11
River goby (*Glossogobius callidus*)	14	17	17	–	–	–	–
Smallmouth bass *(Micropterus dolomieu)*	5	4	5	–	–	–	–
Spotted bass (*Micropterus punctulatus*)	7	7	7	–	–	–	–
Banded Tilapia (*Tilapia sparmanii*)	12	11	13	–	–	–	–
African longfin eel *(Anguilla mossambica)*	1	0	1	–	–	–	–
African sharptooth catfish (*Clarias gariepinus*)	1	0	1	–	–	–	–

cam, underwater camera; snork, snorkel survey; eDNA, environmental DNA; -, no sampling.

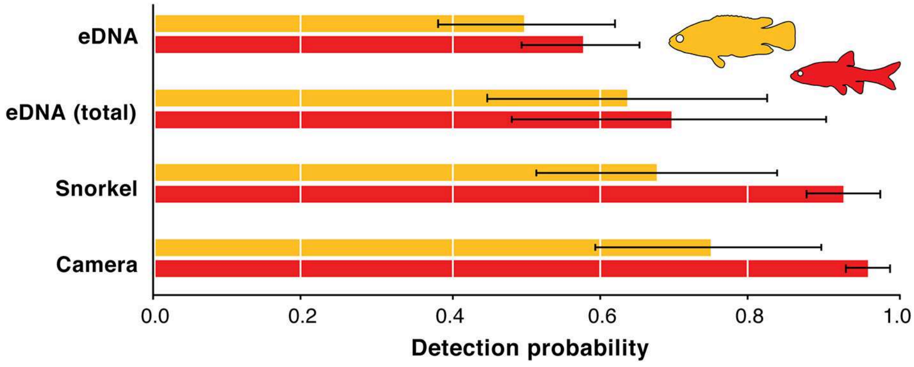

FIGURE 3 | Detection probability model-averaged estimates for underwater cameras, snorkel surveys, eDNA combined replicates, and eDNA replicates for redfins (red) and Cape Kurper (yellow). Error bars represent standard deviations.

an insufficient number of detections of the other fish species across the sampling area. Across the 69 sampling sites, the model-averaged detection probability estimates for the redfins was 0.96 (SD = 0.03) using underwater cameras, and 0.93 (SD = 0.05) using snorkel surveys, 0.70 (SD = 0.21) for combined-replicate eDNA, and 0.58 (SD = 0.08) for eDNA replicates (**Figure 3**). For Cape Kurper, the model-averaged estimates of the detection probability were 0.75 (SD = 0.15) using underwater cameras, 0.67 (SD = 0.16) for snorkel surveys, 0.64 (SD = 0.19) for combined-replicate eDNA, and 0.50 (SD = 0.12) for eDNA replicates (**Figure 3**). For both fishes, eDNA consistently underperformed while underwater cameras had the highest detection probability.

Habitat Variables Affect the Detection Probabilities of the Three Different Methods

To investigate the effect of habitat variables on each sampling method, multi-scale occupancy models were run with covariates hypothesized to affect each method individually and simultaneously while using the top covariate for occupancy. The covariates for the probability of occupancy and detection were pool length, average pool depth and width, surface area, and volume; additional covariates tested for occupancy included number of invasive fish species present and average and dominant sediment size. Further, turbidity was used as a covariate for detection probability.

TABLE 2 | Summary of the model selection using AIC for the occupancy and detection probability of redfins using underwater cameras, snorkel surveys, and combined eDNA.

Model ψ(avg width), θ(.)	AICc	Δi	w_i	K	−2Log(L)
p(camera&snorkel + length, eDNA(turb))	128.50	0.00	0.12	8	110.1
p(m + length)	128.70	0.20	0.11	7	112.86
p(camera&snorkel + surface area, eDNA(turb))	129.75	1.25	0.07	8	111.35
p(camera&snorkel + length, eDNA(.))	129.99	1.49	0.06	7	114.15
p(camera&snorkel + length, eDNA(avg depth))	131.06	2.56	0.03	8	112.66

Top five models are presented.
(.), constant detection probability across sites; m and &, methods-specific detection probability; avg, average; +, covariate effects both methods similarly.

There were four models with a difference in AICc value of <2 for redfins; however, the top model had a higher weight ($w_i = 0.12$) while the other five models had very similar log-likelihood values, indicating little evidence for their support (**Table 2**; Burnham and Anderson, 2002). The top model revealed that the detection probabilities (*p*) of underwater cameras and snorkel surveys differed but were positively influenced by increasing pool length (**Figure 4A**). eDNA detection probability decreased with turbidity (**Figure 4B**). The top occupancy model included the negative affect of pool width on the probability of occupancy (ψ) of redfins.

For Cape Kurper, there were four supported models within 2 AICc values of the top, where the top model had the higher weight ($w_i = 0.24$), while the other models had more parameters and similar log likelihoods, indicating little evidence for their support (**Table 3**). Based on the top model, the detection probabilities of underwater cameras, snorkel surveys, and eDNA differed, but were negatively affected with increasing turbidity (**Figure 4C**). The top occupancy model for Cape Kurper revealed a negative relationship between average pool width and probability of occupancy (ψ).

Strong Correlation Between MaxN and Snorkel Densities

There were significant strong, positive correlations between the abundance estimates collected by both methods for both fish species. For redfins, the Spearman correlation was 0.63 ($p < 0.001$) between MaxN and averaged snorkel counts and 0.83 ($p < 0.001$) between MaxN and the snorkel density. For Cape Kurper, the Spearman correlation was 0.83 ($p <0.001$, **Figure 5A**) between MaxN and average snorkel counts and 0.85 ($p < 0.001$, **Figure 5B**) between MaxN and snorkel density. The log-transformation normalized the distribution of the residuals for the abundance data of redfins but not Cape Kurper. Therefore, linear regressions were only run for redfins, which had significant positive relationships between MaxN and snorkel averaged counts ($r^2 = 0.65$, $p < 0.001$, **Figure 5C**) and MaxN and snorkel densities ($r^2 = 0.62$, $p < 0.001$, **Figure 5D**).

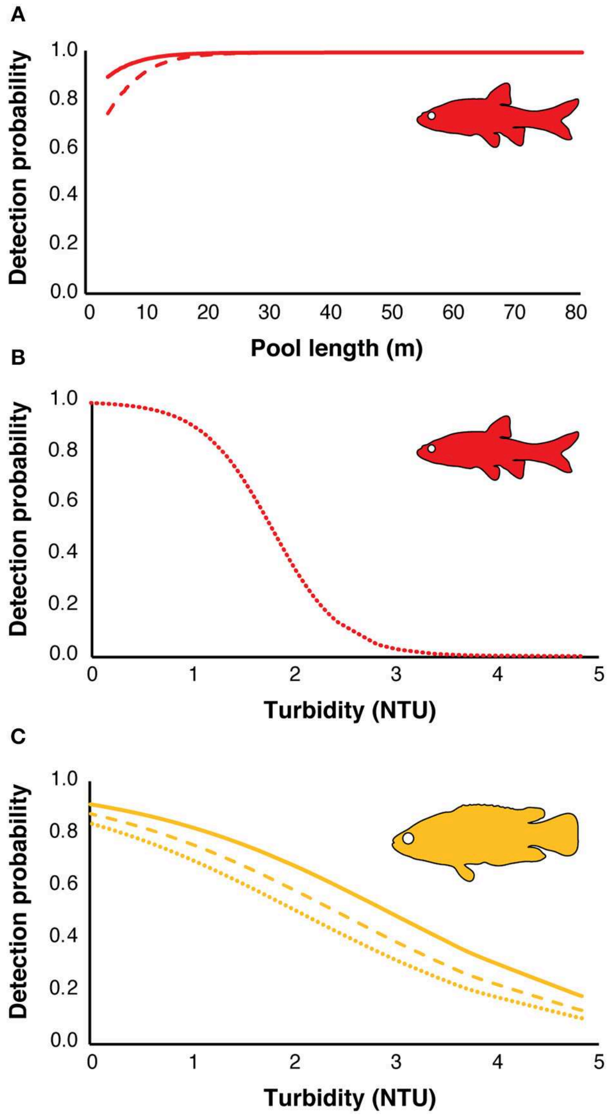

FIGURE 4 | Effect of habitat variables on the estimated detection probabilities from the top models of the three methods for redfins (red) and Cape Kurper (yellow): **(A)** detection probability of underwater cameras (solid line), snorkel surveys (dashed line) against pool length (m) for redfins; **(B)** detection probability of eDNA for redfins (dotted line), **(C)** detection probability of underwater cameras (solid line), snorkel surveys (dashed line), and eDNA (dotted line) against water turbidity (NTU) for Cape Kurper.

Fish Abundance and Pool Morphology Differ Between Tributaries

For both fishes, abundance collected by snorkel survey was significantly higher in the Blindekloof than the other three tributaries (Kruskal-Wallis test, Dunn's *post-hoc* test, $p < 0.05$, **Figures 6A,B**), but that relationship was lost when the count data were converted to densities (m^{-2}, **Figures 6C,D**). The Blindekloof also had the longest, widest, and deepest pools, followed by the Bos, and no significant differences were found between the Fernkloof and Waterkloof (Kruskal-Wallis test, Dunn's *post-hoc* test, $p < 0.05$; **Figure 7**).

TABLE 3 | Summary of the model selection using AIC for the occupancy and detection probability of Cape Kuper using underwater cameras, snorkel surveys, and combined eDNA.

Model ψ(width), θ(.)	AICc	Δi	w_i	K	−2Log(L)
p(m + turb)	157.18	0.00	0.24	7	141.34
p(camera&snorkel + turb, eDNA(avg width))	157.96	0.78	0.16	8	139.56
p(camera&snorkel + turb, eDNA(avg depth))	158.57	1.39	0.12	8	140.17
p(camera&snorkel + turb, eDNA(.))	158.91	1.73	0.10	7	143.07
p(camera&snorkel + turb, eDNA(turb))	159.55	2.37	0.07	8	141.15

Top five models are presented.
m and &, method-specific detection probability; avg, average; +, covariate effects both methods similarly.

DISCUSSION

The model-averaged detection probabilities of the three non-invasive methods were higher for redfins than Cape Kurper and were affected by different habitat covariates. For both fishes, eDNA had the lowest detection probability and was negatively affected by turbidity. However, the model-averaged detection probability for Cape Kurper was similar between snorkel surveys and eDNA. Overall, underwater cameras and snorkel surveys had similar capabilities in detecting the fish community. For the two IUCN-listed fishes, underwater cameras had the highest detection probability compared to snorkel surveys and eDNA. For redfins, the detection probabilities of the visual observation methods were positively influenced by pool length. For Cape Kurper the detection probabilities of the visual observation methods were negatively influenced by turbidity. There were strong correlations between MaxN and abundance estimates, and MaxN and density. However, the linear relationship showed low goodness of fit, making it difficult to directly convert MaxN to absolute abundances.

The detection probabilities of redfins and Cape Kurper using eDNA were the lowest among the three gear types, but it detected both species in all four tributaries. While slightly lower than the visual observation methods, detection probability is within the range of other eDNA studies of rare freshwater species in lotic habitats (e.g., Schmidt et al., 2013; de Souza et al., 2016; Lopes et al., 2017; Bylemans et al., 2019; Sutter and Kinziger, 2019), but was highly dependent upon sampling strategy including volume of water filtered (Wilcox et al., 2016; Cantera et al., 2019; Hunter et al., 2019), number of PCR technical replication effort (Piggott, 2016), size, material, and pore size of the filter (Majaneva et al., 2018), the seasonal hydrology of the system, and rarity of the target (Buxton et al., 2017). Some of these factors, such as rarity, cannot be controlled and are specific to the species under investigation. For example, Wilcox et al. (2016) found that qPCR-based methods could detect a population density of a single fish within a 1 km stretch of river with probability of 0.18, which increased to >0.99 for three fish within a 100 m stretch. Other factors can be mitigated by increasing sampling effort but, as a result, also increase the cost associated with the study. In our study, based on estimates for individual pools and despite an overall lower value of detection probability, the sensitivity of eDNA was such that the scale of detection of both the Cape Kurper and the redfins was effective for detection at the watershed level. For these reasons, eDNA and visual methods may be better suited for detecting species at different spatial scales. The high sensitivity and efficiency of eDNA makes it particularly useful for large rivers. At this scale, eDNA methods outperform conventional sampling methods (Pont et al., 2018), including visual surveys (Lopes et al., 2017; Nakagawa et al., 2018). In contrast, visual observation methods may outperform eDNA when the occupancy of specific pools is of interest. False negatives are more likely for an individual pool, especially if the hydrochemical properties of the pool inhibit the detection of eDNA (e.g., high turbidity; Jane et al., 2015). False positives may be even more problematic at this spatial scale, as eDNA can be deposited in a pool from a source many kilometers upstream (Jane et al., 2015; Balasingham et al., 2017; Pont et al., 2018). The effectiveness of eDNA for characterizing species assemblages across the longitudinal stretch of a river has not been extensively investigated and, because of the many factors contributing to the preservation of eDNA in the water column, may be highly variable across systems (Nakagawa et al., 2018; Pont et al., 2018). In addition, most studies have focused on lentic or marine environments when comparing visual and eDNA methodologies (Yamamoto et al., 2016; Doble et al., 2019). Thus, currently, visual methods may be most appropriate for studies aimed at identifying pools within a river system for rehabilitation or protection, whereas eDNA may be most effective for large scale-studies.

The habitat covariate that had the greatest effect on eDNA detection for both redfins and Cape Kurper is turbidity. Turbidity, a proxy of organic solids containing PCR inhibitors, such as tannic and humic acids, has severe negative effects on the detection of species using eDNA, and increases susceptibility of the survey to false negatives (Harper et al., 2019). PCR inhibitors may also have unpredictable effects on increasing the volume of water sampled (Cantera et al., 2019). The impact of inhibitory substances can be alleviated by diluting samples prior to amplification; however, this practice will also decrease concentrations of target DNA. For rare species, this may dilute target DNA beyond the LOD (Sutter and Kinziger, 2019; Skinner et al., 2020). Methods for removing PCR inhibitors have also been developed (Hu et al., 2015). The detection probability of the Cape Kurper, the rarer species in these pools, is lower for all gear types, which may reflect its lower abundance. However, detection probability with eDNA is comparable for both species, and for the Cape Kurper is comparable to visual methods. This highlights the high sensitivity of eDNA studies, even for rare cryptic species such as the Cape Kurper, while more active and conspicuous species like the redfins might be easier detected with visual methods. Behavioral factors may also impact detection probability using eDNA. For example, differences in shedding rates (Klymus et al., 2015), and activity patterns might also have an impact on the eDNA suspended in the water column (de Souza et al., 2016). The Cape Kurper predominantly swims in short

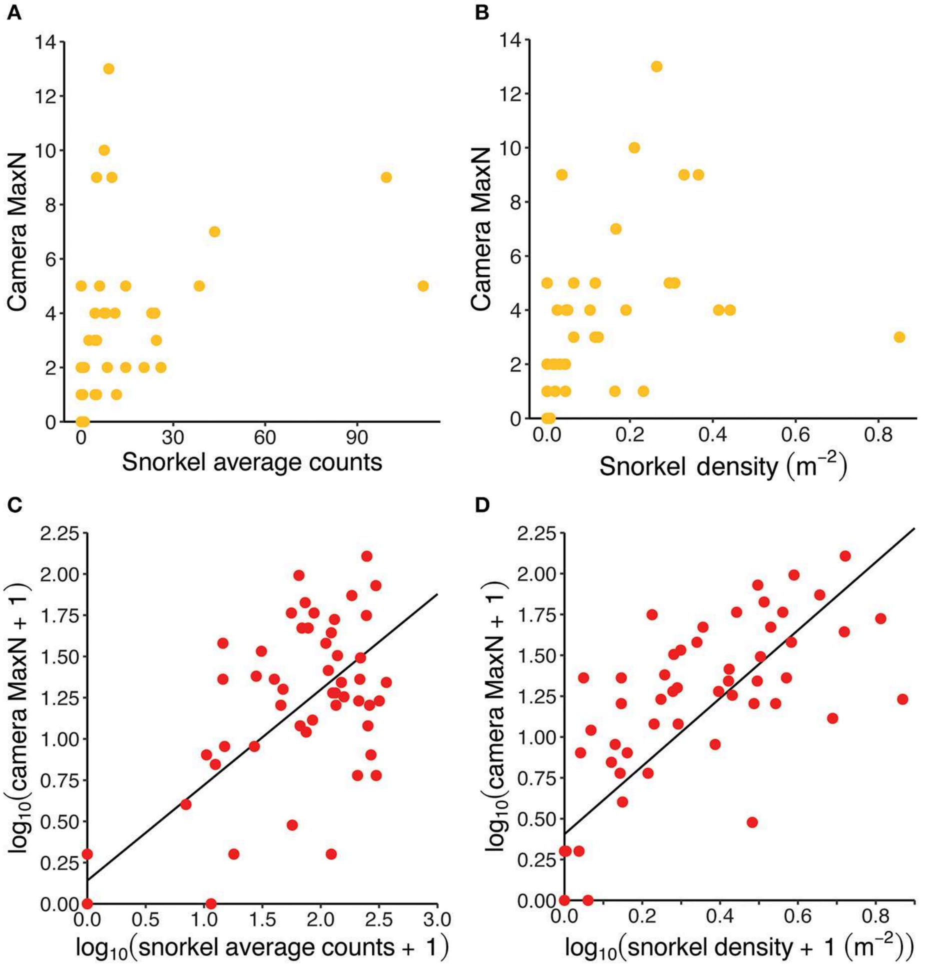

FIGURE 5 | Visualizing the positive correlation between camera and snorkel abundance estimates for Cape Kurper (yellow) and redfins (red): **(A)** MaxN vs. snorkel average counts for Cape Kurper; **(B)** MaxN vs. snorkel density for Cape Kurper; **(C)** log-transformed MaxN vs. log-transformed snorkel average counts for redfins, regression line intercept = 0.14131 (SE = 0.09362) and slope = 0.57897 (SD = 0.05454), $r^2 = 0.65$, $p < 0.001$; and **(D)** log-transformed MaxN vs. log-transformed snorkel density for redfins, regression line intercept = 0.4050 (SE = 0.0770) and slope = 2.0806 (SE = 0.2067), $r^2 = 0.62$, $p < 0.001$.

rapid movements and is more associated with the benthos than the redfins (Kadye et al., 2016). This exemplifies the importance of considering the specific biology of species when designing sampling protocols. For example, Cape Kurper may be more easily detected from sediment samples or water taken from deeper in the water column. Sampling methods combining water samples from different depths (Doble et al., 2019) and sediment samples may improve the detection of specific species, including the Common Carp (Turner et al., 2015), an invasive species found in the same systems in eastern South Africa.

Overall, the sensitivity of our eDNA assay could be improved by increasing the volume of water sampled and the number of biological and technical replicates, and by removing or mitigating the effect of inhibitors; however, this would lead to additional technical challenges associated with transporting or processing water samples, especially for remote localities. In this study, including the detections and non-detections of each eDNA replicate of each pool, instead of using the combined-replicate eDNA detection and non-detections, into the occupancy models reduced the eDNA detection probability by about 20%, revealing that there is a lot of variation in detection across replicates taken from a pool. Increasing the number of physical replicates and the total volume of water sampled should improve detection probability of both species, assuming inhibition of the PCR reaction can be overcome (Cantera et al., 2019). In addition, for these remote locations, filtering on site is also more appropriate to limit degradation of eDNA and reduce effort required to transport samples. Recent methodological advances have made onsite eDNA extraction and PCR-based detection easier, but are not inexpensive (Thomas et al., 2018). Costs associated with acquiring or transporting specialized equipment and the increased personnel hours required to increase sampling effort and onsite processing may be disproportionally high in remote areas.

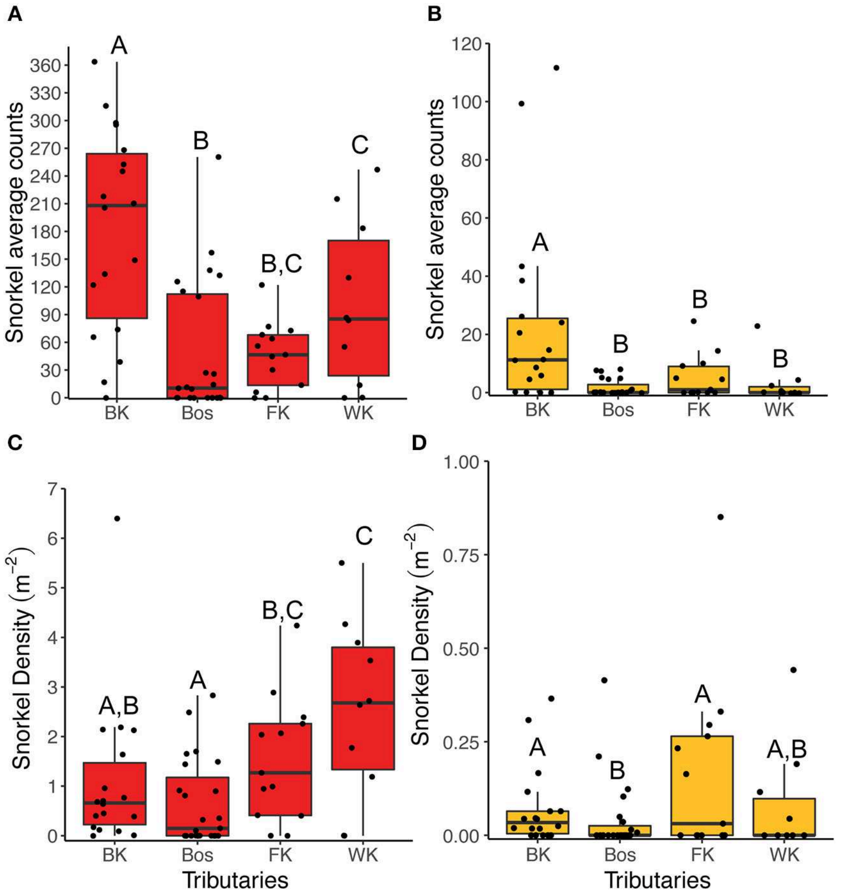

FIGURE 6 | Boxplots of the snorkel abundance data collected for redfins (red) and Cape Kurper (yellow) at each tributary. The snorkel average counts for **(A)** redfins, and **(B)** Cape Kurper. The snorkel densities (m^{-2}) for **(C)** redfins, and **(D)** Cape Kuper. BK is the Blindekloof, Bos is the Bos river, FK is the Fernkloof, and WK is the Waterkloof. Different letters above boxplots represent significant differences ($p < 0.05$) from the *post-hoc* Dunn's test.

The most significant costs associated with processing eDNA samples are associated with the facilities and instruments required for the extraction and PCR (Hinlo et al., 2017). Because of the high risk of contamination, it is essential to maintain two functional lab spaces, one "clean lab" where samples can be extracted and processed separate from the lab where the PCR reactions are undertaken (Goldberg et al., 2016). Therefore, the cost associated with these studies is largely dependent on the accessibility of the required facilities and is many orders of magnitude more expensive than visual methods. These costs shrink as the size of the study increases due to economies of scale and the high-throughput capacity of qPCR assays and next-generation sequencing (Smart et al., 2016). Nevertheless, even if the appropriate facilities for processing eDNA samples are available, methods need to be optimized for the target species, ensuring a minimum acceptable standard for deployment (Klymus et al., 2020), analogous to the MIQE standards in clinical PCR applications (Bustin et al., 2009). Once optimized, these approaches are widely applicable across broad geographic scales, taking into account environmental factors that may influence their efficacy (Cantera et al., 2019). The standardized nature of these studies has made it easier to study wide-spread invasive (Amberg et al., 2015) and commercially valuable fishes (Thomsen et al., 2016), and make detection studies more reproducible (Mauvisseau et al., 2019). In contrast, investigations of new species, typical in understudied localities, require careful optimization of sampling methods, laboratory protocols, and development of species-specific primers. This process can incur unexpected costs as the success of sampling approaches, primers, and protocols can vary unpredictably.

Generally, underwater cameras detected all the same fish species captured by snorkel surveys, although there were slight differences. Cameras detected Goldie Barb and River Goby fewer times than by snorkeling, although the differences were not significant. Nevertheless, differences in detection percentages revealed that underwater cameras did not capture Goldie Barb and River Goby as effectively as snorkel surveys, which may be due to the ecology and morphological characteristics of the fishes. Both the Goldie Barb and River Goby have translucent, light-brown slender bodies (Skelton, 2001) that can be difficult to see and identify in video images. Further, River Goby is a cryptic

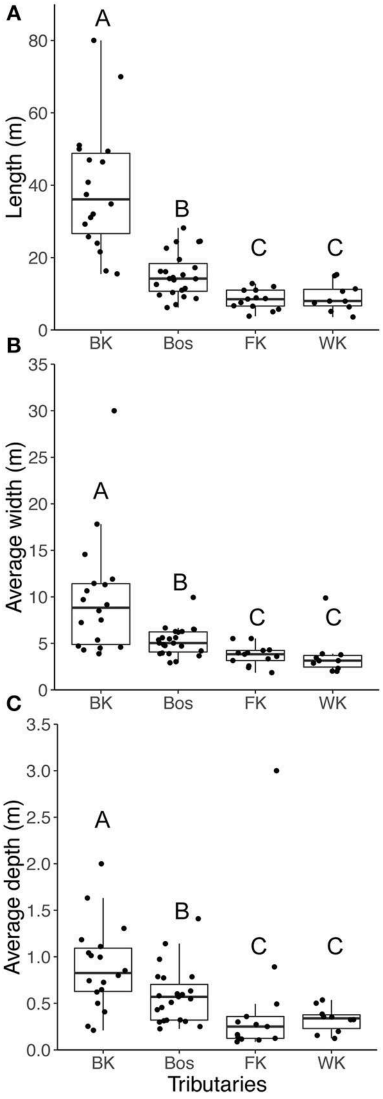

FIGURE 7 | Boxplots for the habitat characteristics for the pools in each of the tributaries, **(A)** length (m); **(B)** width (m); **(C)** depth (m). BK is the Blindekloof, Bos is the Bos river, FK is the Fernkloof, and WK is the Waterkloof. Different letters above boxplots represent significant differences ($p < 0.05$) from the *post-hoc* Dunn's test.

bottom-dwelling fish that tends to remain among cover (Skelton, 2001), making detection using a stationary camera more difficult as cameras rely on animal movement to record encounters (Rowcliffe et al., 2008). The tripod-mounted camera may not be the most effective set up for benthic fishes; a camera pointing toward the sediment mounted on a tow seems to effectively detect and quantify Round Goby, a benthic fish (Schaner et al., 2009; Taraborelli et al., 2009). Although underwater cameras were not as effective as snorkeling in detecting Goldie Barb and River Goby, they detected African Longfin Eel and African Sharptooth Catfish, which snorkel surveys did not. Both of these fishes tend to be more active at night and hide among rocks during the day (Kadye and Booth, 2013; Ellender et al., 2018); therefore, opportunistic sightings of these fishes leaving their shelter when not disturbed (e.g., by a snorkeler) were captured with underwater cameras. To capture the whole community, both diurnal and nocturnal fishing, using visual observation methods, night-time sampling would be required. Ellender et al. (2018) performed night snorkeling with a strong dive flashlight to observe the behavior of native eels, and other studies have used infrared cameras or light attachments on cameras for nocturnal-fish studies (Bassett and Montgomery, 2011; Dirnwoeber et al., 2012; Harvey et al., 2012). Night sampling would require additional personnel hours and extra safety precautions. Alternatively, eDNA could be used to detect the entire fish community with water samples taken from a pool without the necessity to sample at night.

For the endangered redfins, differences were observed in detection probabilities between visual observation methods. The model-averaged estimates revealed that underwater cameras had a higher detection probability and lower variation than snorkel surveys and eDNA. The detection probabilities for underwater cameras and snorkel surveys were above 0.90, suggesting that both methods are very effective at detecting redfins, although these detection probabilities decrease with decreasing pool length. The decreasing detection probability of both visual methods with decreasing pool length for redfins is contrary to what we had hypothesized. Generally, as the spatial scale of an area increased, it became less likely that an animal would be encountered; however, if the number of individuals also increased, then the animal was more likely to be encountered (Rowcliffe et al., 2008). Redfins abundance was highest in the Blindekloof, which also had the longest pools, but density was higher in smaller river pools. If the fish were diluted across the length of the pool as indicated by the density estimation, then detection probability would decrease, as we hypothesized, not increase as the models revealed. However, Redfin tend to form large shoals of over 100 individuals (Skelton, 2001; Ellender et al., 2018), which are very conspicuous and readily detectable by the underwater camera and snorkeler, especially as it is a curious fish that is attracted to the snorkeler (RAC, personal observation). Ellender et al. (2012) found that these two fish species were attracted to the cameras <5% of the time, noting that the behavior does not bias the camera detection data. Therefore, detection probabilities of the visual observation methods are likely being driven by the large schools of redfins in the long pools of the Blindekloof. A study by Castañeda et al. (2020) revealed that underwater cameras had a high detection probability in detecting an endangered minnow that mainly used the water column of a pool, similar to redfins. On the other hand, Cape Kurper does not aggregate in large shoals; thus, its density likely reflects its actual distribution across the pools and the detection probability of both visual observation methods is hypothesized to decrease with increasing spatial scale.

The detection probabilities of the Cape Kurper were lower than redfins for all gear types. The detection probability of underwater cameras for Cape Kurper was 23% lower than that of redfins, while the snorkel survey detection probability was 28% lower. The habitat covariate that drives the detection probabilities for the visual observation methods of the Cape Kurper also differs from that observed for the redfins. Turbidity, not a spatial covariate as with redfins, had the strongest negative effect on the detection probabilities on the two visual methods; as water clarity decreases so does detection probability of the two methods that solely rely on vision to capture fishes. Cape Kurper is more cryptic relative to the large shoals of redfins and tends to hide in structural habitat (Ellender et al., 2012), thus it would be difficult to detect in less clear water. Higher water turbidity also decrease the detection probability of underwater cameras and backpack electrofishing, two visual methods that have been applied for monitoring an endangered minnow in temperate streams in Canada (Castañeda et al., 2020). A study conducted by Ellender et al. (2012) in the Swartkops watershed confirmed that there were no significant differences between the detection rates of underwater cameras and backpack electrofishing for either redfins and Cape Kurper, concluding that underwater cameras are a good non-invasive alternative method.

Estimating abundance and density is required to attain important information on the population ecology of theses fishes; hence, direct comparison between these estimates is necessary. There was a strong correlation between the camera and snorkel data, MaxN increased with both increasing snorkel counts and density. For redfins, log-transformation successfully normalized the data, thus linear regressions could be run. The linear regressions revealed that there was a direct relationship between MaxN and snorkel counts and density; however, the goodness of fit values were low. The goodness of fit values suggests that only about 60% of the variance of MaxN could be explained bysnorkel counts and density. For Cape Kurper, because the data were not normally distributed even with data-transformation techniques, a linear regression could not be run without violating important assumptions. Therefore, no true pattern could be discerned for direct conversion between MaxN and the snorkel data. Furthermore, cameras are static and do not have a spatial reference, unless used in stereo or the distance to a fixed known point is calibrated (Harvey et al., 2002; Struthers et al., 2015) to appropriately convert MaxN to density, resulting in measurement of relative, not absolute, abundance as with snorkeling that covers the whole pool. At most, researchers using underwater cameras can conclude that a higher MaxN recording results in a higher relative abundance of fish, as the positive correlations revealed in this study and the lack of fit between MaxN and density. Generally, MaxN often underestimates abundance while snorkel surveys can be biased based on the behavior of the fishes (Harvey et al., 2002; Campbell et al., 2015). Hence, if absolute abundances are required, then snorkel surveys are better suited than underwater cameras, as the latter could only provide relative abundance estimates, unless multiple cameras are deployed to cover the entire pool.

There are strengths and weaknesses for each method, and researchers must prioritize their conservation needs and resource availability before deciding on which method to use for sampling in remote locations. In clear headwater environments, visual observation methods were better at detecting IUCN-listed fishes than eDNA. Visual observation methods performed best in clear waters as increasing water turbidity decreased the field of view of the snorkelers and cameras; therefore, other non-invasive methods are needed when turbidity is high. However, given that eDNA was similarly negatively influenced by turbidity, it is unsuitable to replace visual observation methods in streams with higher turbidity. For all three methods, depending on the distance between pools, many sites can be sampled in a single day; however, it could take many hours of trained-personnel time to score video data (∼35 min per video, RAC personal observation) and process eDNA samples. Furthermore, electricity, which may not be available in remote field sites, is needed to charge camera batteries, upload video footage to hard drives, and filter eDNA if not using a hand pump. In this study, we used only one camera per pool; however, depending on the research needs and environmental factors, different approaches can be used. For example, the use of two stereo-cameras mounted at a fixed distance, calibrated with a scale bar, can accurately measure the size of fishes for population-structure analysis (Harvey et al., 2002; Harasti et al., 2014), or multiple cameras can be used at a site to increase detection of rare fishes (Castañeda et al., 2020). An additional resource necessary for eDNA at the base camp is a dedicated sterile space for eDNA filtration, which may not be readily available in many remote areas. Personnel trained on sterile filtration technique would be necessary to process the eDNA on site. Nevertheless, eDNA could detect full species community (diurnal and nocturnal fishes) with one visit, unlike the visual observation methods that would require night-time sampling. On the other hand, snorkel surveys require trained personnel in the field to reliably count and identify species in the streams, but the data are immediately available for analysis. However, fish identifications and counts using snorkel surveys are not verifiable unless visually recorded (e.g., GoPro on mask), and information regarding behavior can be difficult to collect without disturbing the fish, as they may be attracted to or repelled by the snorkeler if the snorkeler moves too quickly (Thurow et al., 2012). Specialized fish identification training would be required for field personnel. Snorkel surveys can provide density data while underwater cameras can only reliably provide relative abundance. Generally, eDNA requires the most specialized space and equipment but has the greatest potential for high-throughput assays, once optimized for an ecological community or locality. Underwater cameras are a powerful tool capable of capturing and storing unique information on the behavior and habitat use of fishes but cost more and take more time to complete than snorkel surveys, especially if multiple cameras are needed (Friesen and Chivers, 2006; Domenici et al., 2014; Struthers et al., 2015). The equipment needed to collect the field data for the three methods can easily be transported through rugged terrain with the main limiting factor for the three methods being accessibility to resources in the lab and field.

Researchers are encouraged to use at least one of these non-invasive methods when sampling rare freshwater fishes as they are reliable tools for collecting information on fish ecology in remote areas with minimal negative effects on the populations themselves. Climate change is predicted to increase water temperatures and alter water discharge, which may have negative impacts of the growth and survival of freshwater fishes (Bassar et al., 2016; Reid et al., 2019). Fishes listed on the IUCN Red List are already threatened by other stressors such as habitat degradation and invasive species. The additional threat of climate change may compound or work synergistically with existing threats and exacerbate stress on already vulnerable fishes (Rahel and Olden, 2008; Comte and Olden, 2017; Reid et al., 2019). Using non-invasive sampling methods to reduce unintentional harm during monitoring will become more important as multiple threats continue to impact fish populations and communities. Continual monitoring of vulnerable fish populations is important to understand occupancy and metapopulation dynamics across time and space and to make appropriate inferences on conservation management needs; these non-invasive methods can facilitate long-term monitoring studies without jeopardizing populations. Therefore, these three methods will become of even greater importance as climate change and other stressors continue to negatively impact unique fish communities throughout freshwater ecosystems (Darwall et al., 2018; Reid et al., 2019).

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by SAIAB Animal Ethics Committee University of Toronto Scarborough Local Animal Care Committee.

AUTHOR CONTRIBUTIONS

RC, SC, BE, and OW conceived the project. RC, SC, and BE designed the field protocol and collected the field data. AV and SC completed the eDNA extractions. AV designed and conducted the qPCR protocol and wrote the methods. RC scored the video recordings. RC analyzed and interpreted the data, and wrote the manuscript with assistance from AV, SC, NM, and OW. DH, HM, NM, and OW financially supported, approved, and provided critical advice on the project. All co-authors have revised the manuscript and gave final approval for publication.

FUNDING

We gratefully acknowledge the funding support from NSERC Canadian Aquatic Invasive Species Network II, NSERC Discovery grants to NM, DH, and HM, FRQNT Scholarship to RC, and the Department of Science and Innovation (DSI)/National Research Foundation (NRF) South African Research Chairs Initiative (Inland Fisheries and Freshwater Ecology, Grant No. 110507) to OW.

ACKNOWLEDGMENTS

We would like to thank Carol Blumenthal at the Skilderkrantz Nature Reserve for hosting us during our fieldwork. We would also like to thank S. J. Collins, C. Coppinger, and A. Winkler for their assistance in the field, and K. Wong for help scoring videos. We are grateful for the facilities and lab equipment provided by N. R. Lovejoy and the Center for the Neurobiology of Stress (CNS) at the University of Toronto Scarborough (UTSC). We acknowledge use of infrastructure and equipment provided by the NRF-SAIAB Research Platforms and the funding channeled through the NRF-SAIAB Institutional Support system. We thank Albert Chakona and the NRF-SAIAB collections for providing us with the fin clips and genetic sequences of the fishes in this study.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00029/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 22 April 2020
doi: 10.3389/fenvs.2020.00039

Water Purifying Capacity of Natural Riverine Wetlands in Relation to Their Ecological Quality

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Wetlands are among the crucial nature based solutions for river water purification. The ecological quality of these multi-purposed ecosystems could be disrupted due to overloading of nutrients and other pollutants. We investigated the water purifying efficiency and ecological quality of three natural riverine wetlands located in urban area in southern Ethiopia. Of the three wetlands, Boye wetland is located in a densely populated area with intensive human activity, and the other two, Fisho and Kitto located in a relatively less populated area of Jimma town. We sampled water, macroinvertebrates, and diatoms, to compare sites before joining the wetland, within the wetland and after passing through the wetland. Considering both seasons, up to 74% TP, 73% DIN, and 77% BOD reduction was recorded. The lower concentration of nutrients, and BOD in sites after joining the wetland showed the presence of pollution attenuation. Macroinvertebrate and diatom based bio-indices depicted higher biodiversity and lower relative abundance of tolerant taxa in sites after joining the wetland, which implied the potential of studied wetlands to reduce pollutants and sustain biodiversity. The incoming streams of Boye showed bad water quality and heavily degraded ecological status (Ethbios score 8–10). Most of the sites associated with Boye wetland depicted a major ecological disturbance (Ethbios score < 44). The incoming streams of Fisho revealed moderate (Ethbios score = 58) and poor (Ethbios score = 20) water quality. Most of Fisho sites had a moderate water quality with significant ecological disturbance. Sites associated with Kitto wetland, had a slight ecological disturbance (Ethbios score of 93 and 72) and some with significant ecological disturbance (Ethbios index score between 45 and 59). The wetland fed by heavily polluted streams showed the most degraded ecological quality compared to the other two that are fed by less polluted streams. An RDA model visualized pollution gradient among sites. Generally, this study confirmed the potential of natural wetlands to mitigate nutrients and organic pollutants and sustain biodiversity. However, when the incoming water is heavily degraded, the retention of pollutants seriously affect the wetland's ecological quality.

Keywords: water purification, ecological quality, macroinvertebrates, diatoms, nutrients, organic pollutants

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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *02 September 2019*
Accepted: *18 March 2020*
Published: *22 April 2020*

Citation:
Sileshi A, Awoke A, Beyene A, Stiers I and Triest L (2020) Water Purifying Capacity of Natural Riverine Wetlands in Relation to Their Ecological Quality. Front. Environ. Sci. 8:39. doi: 10.3389/fenvs.2020.00039

INTRODUCTION

Freshwater pollution is one of the worsening environmental issues in the developing countries (Hanasaki et al., 2013; Babayemi et al., 2016), commonly associated with nutrient, organic and inorganic loadings, alteration of hydro-morphology, and habitat degradation (Chen et al., 2016; Sharifinia et al., 2016). Intensive agricultural practices with the application of uncontrolled fertilizers and pesticides and human wastes are the most important sources of freshwater nutrient loading, which mostly occurs in a diffused form and threaten the aquatic ecosystem (Strokal et al., 2016, 2017). Such non-point source pollutants are more challenging for both containment and treatment (Verhoeven et al., 2006). Hence, a sustainable water resource management which can uphold the societal needs while keeping ecological, environmental and hydrological integrity is crucial (Berhanu and Poulton, 2014; Serpa et al., 2014).

Studies are promoting the application of "green" infrastructure and nature-based solutions in water purification (Kumar et al., 2015; Liquete et al., 2016). Wetlands are one of the multipurpose ecosystems, which covers 8–10 million km^2 globally (Lehner and Döll, 2004) and, characterized by a unique hydrology, soil, and vegetation (Huang et al., 2015). Wetlands provide ecological, hydrological and socio-economic benefits (Justus et al., 2016; Liquete et al., 2016; Moges et al., 2016). Previous studies have demonstrated the potential of wetlands to attenuate pollution from agricultural areas, and urban sewage (Díaz et al., 2012; Comín et al., 2014; Bateganya et al., 2015). Wetlands purify water through flow velocity reduction, microbial degradation of organic matter, microbial transformation, and nutrient retention and uptake by plants (Vymazal, 2007; Moreno-Mateos and Comin, 2010).

However, wetlands could be overloaded due to excessive nutrients and other contaminant inputs, thus the ecosystem may shift into another stable state; from being a sink to a source of pollutants (Verhoeven et al., 2006; Resende et al., 2010). This might result in loss of ecological quality and a shift in diversity, and composition of taxa (Hansson et al., 2005; Davidson et al., 2012).

In Ethiopia, wetlands are estimated to cover about 1.4% of the country's landmass (Gebresellassie et al., 2014). Like in many other African countries (Beuel et al., 2016), wetlands in Ethiopia are under continuous pressure of degradation (Mereta et al., 2012; Moges et al., 2016). Such problems are aggravated by rapid population growth in the absence of adequate sanitation facility and improper wastewater management (Bateganya et al., 2015). For instance, in eastern Ethiopia, people kept putting pressure on lake Haramaya until it vanishes (Mengisteab, 2012; Abebe et al., 2014). Other research reports indicated the degradation of, for instance "Boye" and Gilgel-Gibe wetlands (Van der Bruggen et al., 2009) and the complete dry out of "Aba Samueal" marsh (Gizaw et al., 2004). Other researchers also warn similar incidents could happen to other wetlands in the country if proper measures are not in place (Bekele et al., 2001; Beyene et al., 2012). An integrated approach should be used to assess ecological status and ensure the functioning of wetlands and, therefore to monitor and protect these multi-purpose ecosystems (Justus et al., 2016). In order to monitor the water quality, physicochemical parameters are important variables. They provide information about the status of the water during the sampling event (Resende et al., 2010). Additionally, biological indicators provide information on the general ecosystem and they can trace back past environmental variability. The biological integrity of an ecosystem is informative about the system's ability to support and sustain biodiversity (Lakew and Moog, 2015). Biological communities, particularly macroinvertebrates and diatoms, are effective to assess the level of disturbance and the overall ecological status of an aquatic ecosystem.

Wherever possible in water quality assessment, simultaneous use of two or more biological quality elements including macroinvertebrates, fishes, macrophytes, planktons, and diatoms is recommended to provide an integrated measurement of the overall ecological status. Researchers recommended the use of two or more suitable groups contemporaneously so that one can compensate the limitations of one group with the strength of the other (Carlisle et al., 2008; Torrisi et al., 2010; Lainé et al., 2014). However, for extremely high turbidity in the water system which is the case in our study area, fish and macrophytes are either absent or contain a very limited number of species to be used as bioindicators for ecological quality assessment (Krstic et al., 2007; Beyene, 2010). The simultaneous use of diatoms and macroinvertebrates reported to give good indication of ecological quality in freshwater (Resende et al., 2010; Justus et al., 2016).

Macroinvertebrates are indicators of choice to assess the presence of catchment disturbance and hydro-morphological alterations (Birk et al., 2012; De Troyer et al., 2016). Their ecology is well determined and responds sensitively to environmental gradients (Lakew and Moog, 2015). Diatoms community composition is more related to the water quality (Sonneman et al., 2001; Rimet et al., 2005). Different diatom species have their own distinct habitat preferences (Vilmi et al., 2015) which made them ideal to predict ecological quality. Beyene et al. (2009) suggested diatoms as powerful indicators of gradients of pollution in tropical freshwater ecosystems. These two bioindicators, macroinvertebrates and diatoms, are considered as complementary tools to assess water quality, and ecological status of the aquatic ecosystem (Feio et al., 2007; Resende et al., 2010).

This study used both bioindicators, diatoms, and macroinvertebrates, in relation with physicochemical variability to provide a complimentary insight on the ecological quality of the system under study. Since there is variation in hydrological variables during the wet and dry season, research in tropical water bodies should deal with seasonality (Beyene et al., 2014). In this study, we also consider the seasonal variation in water quality.

Although there are studies dealing with the water purification potential of wetlands (Vymazal, 2007; Fountoulakis et al., 2009; Mereta et al., 2012), both natural and constructed, or its ecological status, both of these aspects are seldom studied together. These two aspects should be studied together in order to design a wetland management tool which enhances the application of wetland ecosystems for *in situ* water purification without risking its ecological quality. Therefore, the main objective of this study is to determine the efficiency of natural riverine wetlands to reduce nutrient and organic pollutant concentrations, and to assess their ecological quality in relation to the incoming river water quality status. The specific objectives of the study are hence (a) to evaluate the efficiency of the three riverine wetlands in reducing pollution, (b) to assess the ecological status of incoming and outgoing streams to and from three natural riverine wetlands, and (c) to investigate the impact of the different incoming streams on the ecological quality of the wetlands themselves using physicochemical parameters and two (diatom and macroinvertebrates) biological quality elements.

MATERIALS AND METHODS

Study Sites and Samples

The study site is located in Jimma, south western part of Ethiopia, between the geographic coordinates of 7°41′N and 36°50′E. The study area has an elevation of 1,704 m above sea level (Duguma et al., 2012). For this study, three riverine wetlands were selected namely; Boye (B), Kitto (K), and Fisho (F) wetlands (**Figure 1**). These wetlands are considered as urban influenced (Moges et al., 2016). However, the level of disturbance differs among the wetlands. Boye wetland is located in the most populated area of Jimma town with heavy anthropogenic activities. It is estimated to cover 60 ha area (Moges et al., 2016) on average. The major anthropogenic disturbances in this wetland, as observed during the field survey, include solid and liquid waste disposal, car washing, livestock grazing, and papyrus harvesting. There are four main streams flowing into Boye wetland, namely Kochie (B1), Dololo (B2), University (B3), and Awaitu streams (B4). All of these streams serve as a waste dumping sites for the respective residents. They discharge all kinds of wastes without any form of prior treatment. These streams confluence within the wetland and flow to Gilgel Gibe River. Fisho and Kitto wetlands are located in a relatively less populated area of the town with different types of disturbances. The streams feeding them are also relatively less stressed compared to those that feed Boye wetland. Fisho wetland is estimated to cover 40 ha area. Two streams join Fisho wetland namely, Degoye 1 (F1) and Degoye 2 (F2). Brick mining, farming, clothes washing, and livestock grazing are the major disturbances in Fisho wetland. Kitto wetland with 50 ha estimated area, has two streams flowing into it. One is Kitto River (K1), located in the upstream of the wetland with most of its catchment upstream of the town, which is the least disturbed site, and the second stream (K2) is a merge of small streams passing through residential areas. The major anthropogenic activities in Kitto wetland site are cloth washing, swimming, and plant harvesting (especially papyrus). All the feeding streams were permanently flowing. However, their flow rate extremely decreased during the dry season.

A total of 20 sampling sites, including the streams associated with the wetlands, were selected to analyze the water purifying effect of the wetlands and their ecological status. Sampling locations before joining the wetlands were; B1, B2, B3, B4 (all four streams that join Boye wetland), F1, F2 (the two streams that feed Fisho wetland), K1 and K2 (the two streams feeding Kito wetland). Those with in the wetland were B5, B6, B7 (from Boye wetland), F3, F4 (from Fisho wetland), K3 and K4 (from Kito wetland). The sites immediately after passing through each

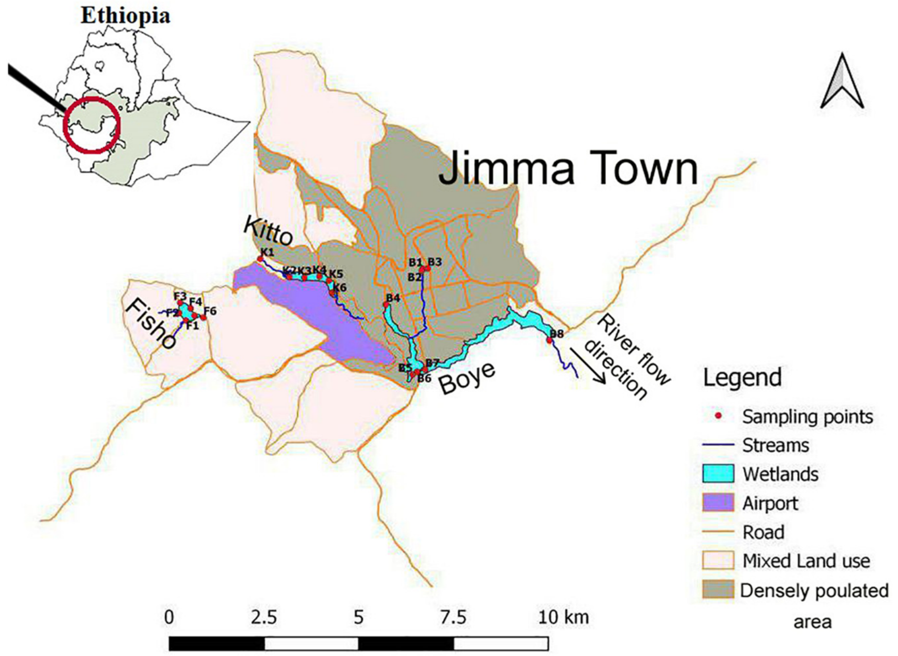

FIGURE 1 | Map of the study area including sampling locations in three natural riverine wetlands of Jimma, southwest Ethiopia (Namely; Boye (Sampling points starting with "B"), kito (that start with "K"), and fisho (points starting with "F"); and the respective incoming streams that fed those wetlands together with the outflows of the three wetlands (see **Supplementary Table S1** for the site code descriptions). The indicated flow direction represents all the three wetlands in the study map.

wetland were B8, F5, F6, K5, and K6. To deal with the seasonal variations in hydrological processes of tropical water bodies (Beyene et al., 2009), water samples, macroinvertebrates, and diatoms were sampled in replicates and duplicates, when access is difficult, in August (2016) and February (2017) representing the wet and dry seasons, respectively.

Measurement of Environmental Parameters

Dissolved oxygen (DO), water temperature, pH, and electrical conductivity were measured using a multi-probe meter (Hach-Model-HQ30d Single-Input, Multi-Parameter Digital Meter) and turbidity was measured using a Wag-WT3020 turbidity meter on-site. We filtered the water samples onsite using Whatman glass microfiber filters (25 mm Ø) and collected in polyethylene bottles of 100 ml for nutrient analysis (nitrite, nitrate, ammonium, and soluble reactive phosphorus). Well-mixed unfiltered water samples were collected using polyethylene bottles for total nitrogen (TN), total phosphorus (TP), total suspended and dissolved solids (TSS and TDS), chloride and alkalinity. The water samples for BOD analysis were collected by inserting clean polyethylene bottles of 1 L to a 30 cm depth in the opposite direction of the current flow of the rivers and immediately sealed and closed. The water samples were transported in a cold box to the laboratory of Environmental Health Sciences and Technology, Jimma University, Ethiopia. The samples were immediately put in to cold box and kept in freezer until the analysis. Generally, the samples were analyzed following standard methods described by APHA (2005). Environmental variables, total nitrogen (TN) and phosphorous [both soluble reactive (SRP) and total (TP)] were measured by Kjeldahl Nessler and ascorbic acid methods, respectively following APHA (2005). Biochemical oxygen demand (BOD) was measured using the azide modification of the Winkler's titrimetric method by determining DO contents of the samples before and after 5 days' incubation at 20°C. High (0.3–30 mg/l) and low (0.01–0.5 mg/l) ranges of nitrate were measured using the cadmium reduction method of 8039 and 8192, respectively. We also used Nessler method 8038 for the determination of Ammonium-Nitrogen following the HATCH water analysis hand book of the USEPA available online for free[1].

Macroinvertebrate Sampling and Identification

Macroinvertebrate habitats were detached by kicking the bottom sediment of the wetlands and in between vegetation and the river bed continuously for about 5 min within 10 m stretch. The dislodged macroinvertebrates were collected using a rectangular frame, 50 × 33 cm, kick net with a 250 μm mesh size. Then the content of the net was transferred into a white tray, sorted on-site using forceps and kept in vials containing 80% ethanol, and labeled with the site code. This procedure was performed twice for each of the 20 sampling locations, and samples were pooled together in a vial for each site. All the samples in the vials were transported to the biological laboratory of Environmental Health Science and Technology department, Jimma University, where we did the identification. Finally, the macroinvertebrates were identified to a family level, except for *Hirudinae* (which was identified as a sub-class) using a binocular microscope and standard identification keys of Tachet et al. (2010) and Bouchard (2004).

Diatom Sampling, Processing, and Identification

Diatom assemblages were sampled simultaneously with macroinvertebrates and water samples. From each of the sampling locations two types of substrates, stone, and hardwood, were scraped using a toothbrush and pooled to a 50 ml polyethylene vial. In the absence of stones, we collected submerged vegetation to clean off the diatoms attached to it. Diatom samples were fixed with 4% formalin and transported to the biological laboratory of Jimma University, Department of Environmental Health Science and Technology.

Diatom samples for species level identification are mostly digested using concentrated H_2SO_4 and HNO_3 according to Lange-Bertalot (2000) and Round et al. (2007). A concentrated acid oxidation method modified from Stevenson and Bahls (1999) was used for the cleaning of diatom frustules. The major modification in the diatom sample processing is the use of HCl as a pre-cleaning in order to remove calcium from the sample.

Slides were prepared by mounting 30 μl from a known volume of digested sample using Zyrax mounting media. Diatom identification and counting was done using a Carl Zeiss light microscope with 1,000× magnification. A minimum of 300 diatom valves were counted in each slide except for some samples from the wet season, where less than 300 diatom assemblages were found. The diatom valves were identified to the smallest possible taxonomic level using different standard identification keys (Lange-Bertalot, 1980, 2001, 2011; Krammer and Lange-Bertalot, 1986, 2000; Taylor et al., 2007).

Statistical Analysis

All the analyses were done using R statistical software (R Core Team, 2015, version 3.2.2) except for diatom indices, which was done using OMNIDIA version 5.2. Packages used in the analysis include Vegan (Oksanen et al., 2015), Packfor (Dray et al., 2013), Hmisc (Harrell et al., 2015).

Descriptive statistics were used to determine the overall status of the water chemistry along the sampling locations. All environmental parameters, except pH, were log-transformed [log (x + 1)] prior to analysis. Distribution of environmental parameters in each group was tested using Shapiro–Wilk test, which is the most powerful normality test (Razali and Wah, 2011). The normality was not attained in all groups, for the parameters under study, therefore non-parametric tests were used for the proceeding analysis. A Kruskal–Wallis rank sum test and Wilcoxon rank-sum test were used to determine the presence of a significant difference in environmental parameters among the three wetland sites and between the two seasons, respectively. The Kruskal-Wallis test was followed by Mann-Whitney test to

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[1] https://www.hach.com/wah

make a pairwise comparison. Bonferroni correction was applied to correct for multiple testing in order to reduce the chance of type I error. Spearman correlation analysis was done to determine the association between environmental variables and biological indices using the Hmisc package.

Percent Change Calculation

The potential of wetlands to reduce or remove nutrients and organic pollutants was calculated, for TP, PO_4-P, NO_3-N, NH_4-N, DIN, TN, EC, and BOD, using the following equation:

$$\%Change = \frac{C_{in} - C_{out}}{C_{in}}$$

where C_{in} represent the incoming concentration and C_{out} for the outgoing concentration.

For the wetlands having multiple inflows, the mean concentration of the inflows was taken as the incoming concentration (C_{in}).

Ordination Analysis

Macroinvertebrate taxa and diatom taxa abundance data were Hellinger transformed prior to proceeding analysis. In order to choose between linear, Principal Components Analysis (PCA), Redundancy Analysis (RDA) or unimodal; Correspondence Analysis (CA) models, Detrended Correspondence Analysis (DCA) was applied on the macroinvertebrate and diatom taxa count data. The maximum gradient length of the four ordination axis was between three and four in both cases (macroinvertebrates and diatoms), during both seasons (wet and dry season). The gradient didn't show the dominance of either linear or unimodal gradients. Hence, we applied both RDA and CCA to select the one which explains better, and RDA was chosen as it was the best from the two. RDA model was built by a forward selection procedure (permutation, n = 999) using double stopping criterion to investigate the relation between macroinvertebrate and diatom taxa with environmental variables. For each season, dry and wet, the RDA model was built for the three wetland sites together.

Compositional and Diversity Metrics

Macroinvertebrate and diatom-based compositional and diversity metrics were calculated to describe the community structure of diatoms and macroinvertebrates in each site, for both seasons.

Total taxa richness, Shannon's diversity, % filter collectors (FC), and Ethbios index were calculated based on macroinvertebrate community assemblage. Total taxa richness and %FC are among the recommended indices to assess the ecological quality of wetlands in Ethiopia (Mereta et al., 2013). Shannon's diversity is among the commonly used indices in ecological studies and it accounts for abundance and evenness (Magurran, 2013). Ethbios index is a recently developed index similar to biological monitoring working party (BMWP) but includes those macroinvertebrate taxa which are endemic to Ethiopia. The Ethbios is designed mainly for river systems of Ethiopia. To use it for the sampling sites from the wetlands we tried to verify it with the MMI developed for Ethiopian wetlands by Mereta et al. (2013). In determining the Ethbios index, each taxon is assigned a score based on its sensitivity to pollution; highest value for highly sensitive taxa and low values for pollution tolerant ones. The overall Ethbios index value of the site was obtained by summing up the scores for each taxon (Lakew and Moog, 2015).

Diatom based metrics were also used to have a comprehensive insight about the ecological quality of the system under study. The calculated indices include Shannon's diversity, total taxa richness, and the relative abundance of pollution tolerant taxa (% PT).

RESULTS

Spatiotemporal Variation of Environmental Parameters

Water temperature (T°), pH, Electrical Conductivity (EC), Total phosphorus (TP), ortho phosphate (PO_4-P), and BOD ($p = 0.001$) were significantly higher in dry season compared to wet season (Mann-Whitney, n = 20) (**Table 1**). Considering the dry season; TN, TP, pH, PO_4-P, NH_4-N, and EC were higher in Boye (urban downstream), compared to Fisho (urban upstream) and Kitto (urban upstream) wetland sites (Kruskal-Wallis, $p = 0.005$; Mann-Whitney, $P < 0.05$) (see **Supplementary Table S2** for exact p-values, and W). BOD ($p = 0.04$) and DO ($p = 0.04$) were significantly higher in Fisho than Kitto wetland sites (Mann-Whitney). During the wet season, the measured environmental variables didn't show a significant difference among sites except for turbidity (Kruskal-Wallis, $p = 0.003$), which is found to be higher in Boye wetland (Mann-Whitney, $p < 0.001$).

Purification Capacity of Natural Riverine Wetlands

The sites from the three wetlands were pooled together as those before joining the wetland, within the wetland, and after passing through the wetland. The pooled values of environmental parameters indicated the presence of pollution gradient. In the dry season, significantly lower concentration of TN ($W = 0$, $p = 0.03$), DIN ($W = 1$, $p = 0.02$), TP ($W = 0$, $p = 0.03$), and PO_4-P ($W = 0$, $p = 0.03$), was observed in sites after draining through the wetland than sites before joining the wetland (Mann-Whitney Wilcoxon). Considerably higher concentrations of NO_3-N and DO, and lower BOD was recorded within the wetland (see **Supplementary Figure S1**).

Percent reduction analysis exhibit variation among studied wetlands. During the dry season, Boye wetland showed the highest percent reduction of TP (74%), whereas Fisho and Kitto wetlands showed 23 and 26% reduction, respectively. The highest reduction of TN (43%) and BOD (18%) was recorded in Fisho wetland (**Figure 2** dry season and **Supplementary Table S3**).

Concerning NH_4-N and NO_3-N, the highest reduction was 34 and 88% in Fisho and Kitto wetland respectively during the dry season (**Supplementary Table S3**). In the wet season, the highest percent reduction of BOD was recorded in Boye wetland;

TABLE 1 | Comparison of physicochemical water quality parameters between the dry and the wet seasons in each of the three wetlands and among Boye, Kito, and Fisho wetlands of southwestern Ethiopia using Mann-Whitney and Wilcoxon rank-sum tests, respectively.

	Boye wetland		**Fisho wetland**		**Kitto wetland**	
Parameters	**Dry (n = 8)**	**Wet (n = 8)**	**Dry (n = 6)**	**Wet (n = 6)**	**Dry (n = 6)**	**Wet (n = 6)**
T°(°C)**	25.9 (1.2)	22.1 (0.6)	24.3 (0.3)	23.6 (1.2)	22.6 (1.0)	21.4 (0.4)
pH***	8.51 (0.10)a	7.62 (0.11)	7.72 (0.17)b	7.22 (0.20)	8.12 (0.18)b	7.36 (0.06)
EC (μs/cm)**	417 (116)a	149 (34)	141 (25)b	76 (4)	185 (10)b	80 (1)
TUR (NTU)	35.1 (6.3)	106.3 (43.9)	26.3 (2.8)	32.5 (7.1)	19.7 (6.9)	21.0 (2.5)
TP (mg/l)*	0.96 (0.58)a	0.56 (0.24)	0.03 (0.01)b	0.17 (0.01)	0.06 (0.02)b	0.18 (0.02)
PO$_4$ (mg/l)**	0.67 (0.52)a	0.13 (0.03)	0.001 (0.001)b	0.06 (0.01)	0.003 (0.002)b	0.04 (0.01)
TN (mg/l)	9.39 (5.02)a	2.64 (0.64)	1.71 (0.38)b	3.00 (1.74)	2.04 (1.16)b	0.97 (0.14)
NO$_3$-N (mg/l)	0.53 (0.31)	1.11 (0.23)	0.26 (0.2)	0.30 (0.09)	0.56 (0.32)	0.47 (0.07)
NH$_4$-N (mg/l)*	2.29 (0.70)a	0.11 (0.01)	0.14 (0.02)b	0.08 (0.02)	0.07 (0.03)b	0.1 (0.002)
DO (mg/l)	3.12 (1.24)ab	4.33 (0.68)	4.30 (0.79)b	4.74 (0.36)	2.11 (0.93)a	3.28 (0.22)
BOD (mg/l)***	38.5 (18.3)ab	7.1 (1.7)	20.3 (3.7)b	3.4 (0.6)	57 (0.1)a	1.2 (0.3)
Cl$^-$ (mg/l)	2.62 (0.2)	3.28 (0.63)	10.25 (2.55)	26.8 (12.18)	26.83 (12.18)	9.37 (2.87)

*All results are in mean and SE (indicated in brackets) of all the sites in a wetland system per season. *Shows significant seasonal difference where, *$P < 0.05$, **$P < 0.005$, ***$P < 0.001$ (Wilcoxon rank-sum test). "a" and "b" indicate significance difference among sites (Mann-Whitney). T, water temperature; EC, Electrical Conductivity; TUR, Turbidity; TP, Total Phosphorus; TN, Total Nitrogen; DO, Dissolved Oxygen; BOD, Biological Oxygen Demand.*

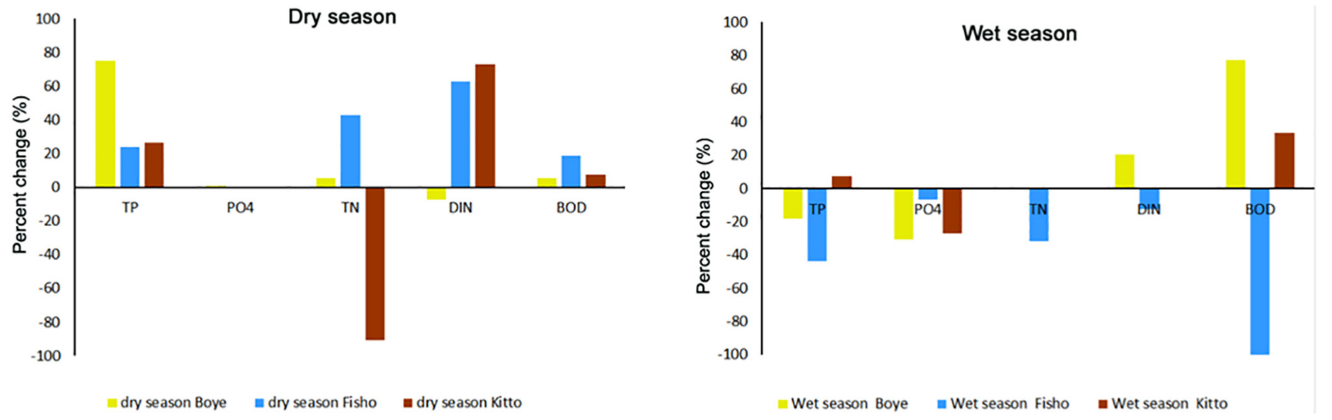

FIGURE 2 | Percent change of nutrients and BOD by natural riverine wetlands of southwest Ethiopia (Namely; Boye, Fisho, and Kitto wetlands) during dry and wet season. TP, total phosphorus; PO$_4$, orthophosphate; TN, total nitrogen; DIN, dissolved inorganic nitrogen; BOD, biochemical oxygen demand (see **Supplementary Table S9** for measured parameters for each site during both the dry and wet seasons).

77%, followed by Kitto wetland; 33% (**Figure 2** wet season and **Supplementary Table S3**).

Composition and Diversity of Macroinvertebrates

A total of 57 macroinvertebrate families were identified during wet and dry seasons. Total taxa richness of Boye was significantly lower than Kitto (Mann-Whitney, $p = 0.001$). The minimum taxa richness of five was recorded in Boye stream (B2). The highest Shannon's diversity value was recorded in Kitto compared to Boye and Fisho wetland sites. The relative abundance of filter collectors (%FC), was significantly lower in Boye than Fisho, and Kitto wetland sites (Mann-Whitney, $p < 0.01$). No filter collectors were found in Boye wetland sites before joining the wetland (B2, B3, B4), except in B1 (**Figure 3**).

The Ethbios index was also lowest in Boye wetland sites. The incoming streams of Boye (B1, B2, B3, and B4) showed bad water quality and heavily degraded ecological status (Ethbios score 8–10). Most of the sites associated with Boye wetland depicted a major ecological disturbance (Ethbios score < 44). Fisho sites had a moderate water quality with significant ecological disturbance. The incoming streams of Fisho revealed moderate (Ethbios score = 58) and poor (Ethbios score = 20) water quality. Two sites (K1 and K5) associated with Kitto wetland, had a slight ecological disturbance (Ethbios score of 93 and 72, respectively) and some with significant ecological disturbance (Ethbios index score between 45 and 59) (see **Supplementary Table S4**).

As shown in **Figures 3A–C**, the pooled value of sites before joining the wetland, within the wetland, and after passing through the wetland, presented a clear gradient in taxa richness, Ethbios

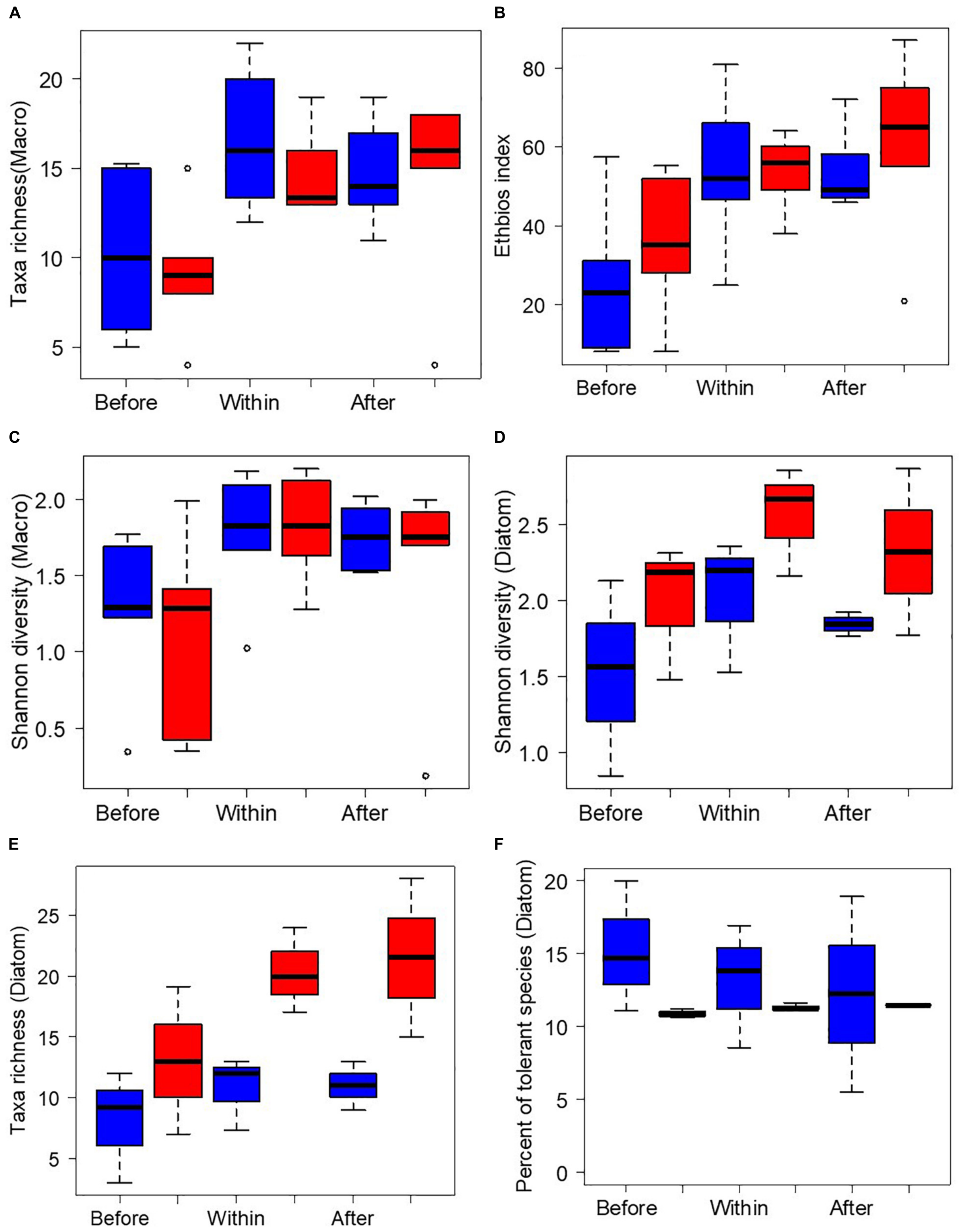

FIGURE 3 | Diversity and compositional metrics of macroinvertebrates: **(A)** taxa richness, **(B)** Ethiobios index, **(C)** Shannon diversity and diatoms: **(D)** Shannon diversity-diatom, **(E)** taxa richness-diatom, **(F)** percent of tolerant species in sites before joining the wetlands ("before"), within the wetlands ("within"), and after passing through the wetlands ("after") in both dry (color: blue) and wet (color: red) seasons. The values are extracted from all the three wetlands i.e., "Boye," "Fisho," and "Kito" wetlands and the mean values are used.

index, and Shannon's diversity index values. The values of all three biotic indices were lowest in sites before joining the wetland.

Composition and Diversity of Diatoms

From both seasons, dry and wet, a total of 101 diatom taxa were identified. Diversity and composition varied among the three wetlands. A minimum of five and maximum of 29 diatom taxa was recorded in Boye (B5) and Kitto upstream (K1) respectively. In general, Boye sites showed significantly lower taxa richness than Kitto sites. Shannon's diversity index value was significantly lower in Boye than Fisho and Kitto wetland sites. Percent of tolerant taxa (% PT) was significantly different among the three wetland sites (Kruskal-Wallis, $p = 0.001$). Boye had the highest percent pollution tolerant taxa ($p < 0.01$) followed by Fisho ($p < 0.01$) and Kitto. A significant difference was observed between the three groups (Kruskal-Wallis, $p = 0.001$).

The pooled value of sites, before joining the wetland, within the wetland, and after passing through the wetland (**Figures 3D–F**), revealed a higher taxa richness of diatoms in sites after joining the wetland during both seasons. However, the taxa richness was higher during wet season than the dry season. The Shannon's diversity was the lowest and percent pollution tolerant taxa was the highest in sites before joining the wetlands than those within the wetland and after passing through the wetland.

Environmental Gradient and Macroinvertebrate Community Assemblage

In the dry season, the redundancy analysis (RDA) model selected NH_4 ($p = 0.005$), TN ($p = 0.005$), and DO ($p = 0.035$) as set of significant variables determining the distribution of macroinvertebrate families. The model explained 58.8% of the taxa-environment relation, where the first axis explained 29.7% and the second axis explained 24%. The overall model was significant with a p-value of 0.005 (Monte Carlo permutation test, $n = 999$). The first axis of RDA (**Figure 4**, Dry season) showed a pollution gradient. This axis was positively correlated with PO_4 and negatively correlated with DO. Streams feeding Boye wetland (B1–B4) were characterized by high PO_4 and TN and associated with the dominance of *Culicidae* (clu), *Syrphidae* (syr), *Chironomidae* (chi), and *Oligochaetes* (oli). In the negative first axis, sites of Boye located within the wetland (B5–B7) and at the outlet point (B8) were characterized by high turbidity. The dominant macroinvertebrates in these sites were *Dytiscidae* (dyt), *Belostomatidae* (bel), *Corixidae* (cor), *Coenagrionidae* (coa), *Veliidae* (vel), *Hydrophilidae* (hyd), *Hirudinea* (hir), and *Notonectidae* (not). Axis 2 (24%) showed a pH and NH_4 gradient. It separated Fisho (F) sites, except F5, along with high level of NH_4 and lower pH. In the dry season, the dominant taxa in this sites were *Sphaeriidae* (sph), *Naucoridae* (nau), *Caenidae* (ca), and *Libellulidae* (lib). Kitto sites (K2, K3, K4, and K6) were grouped together with F5. The upstream of Kitto wetland (K1) was characterized by low level of PO_4, and K2, K3, and K6 are positively correlated with PO_4.

During the wet season, NO_3 and TN were selected as the set of important variables associated with the distribution of macroinvertebrates (Monte Carlo permutation, $n = 999$, $p = 0.005$). Axis 1 (38%) and axis 2 (26%) of RDA (**Figure 4**, Wet season) showed nutrient and pollution gradient respectively. Boye sites were characterized by high dissolved inorganic nitrogen (DIN) and BOD, whereas, Fisho sites were negatively correlated with DIN and BOD. The first axis grouped Boye sites into two, those sites before Joining the wetland (B1, B2, B3, and B4), being in one group and sites within the wetland (B5, B6, and B7) and at the outlet point (B8) being in the other group. The first group (B1–B4) are positively correlated with NO_3, BOD, TN, and DO. Unlike the dry season, *Simuliidae* was abundant in Fisho sites (highly abundant in F4) during the wet season. *Potamonidae* dominated the upstream (F1) of Fisho wetland.

Environmental Gradient and Diatom Community Assemblage

In the redundancy analysis (RDA) model of the dry season that was built using a forward selection with a maximum permutation of 999, the set of important environmental variables determining the distribution of diatom taxa were pH ($p = 0.02$) and EC ($p = 0.02$). The overall model was significant in explaining the taxa-environment relationship ($p = 0.01$). The RDA model explained 71% of taxa-environment relation by the first two axes.

Axis 1 (47.8%) showed pH and NH_4 gradient and axis 2 (23.9%) implicated a pollution gradient (**Figure 5**, Dry season). The first axis separated Boye sites from others. Boye sites (B2, B4, B6, and B7) were positively correlated with high pH and high EC. The diatom taxa dominating these sites are *Eolimna subminiscula* (EM), *Craticula ambigua* (CAB), *Craticula accomoda* (CC), *Navicula gregaria* (NR), *and Gomphonema parvulum* var. *parvulum* (GR). Fisho sites (F1, F3, and F4) were rich in NH_4-N and dominated by *Gomphonema affine* (GA), *Gomphonema parvulum* (GL), and *Navicula cryptocephala* (NY). They were associated with low pH and EC. Except for K1, Kitto sites were grouped together with F2 and dominated by *Eunotia minor* (EN), *Navicula arvensis* (NV), *Gomphonema minutum* (GN), and *Eunotia pectinalis* (EC). The dry season RDA separated Kitto upstream (K1) which was dominated by *Gomphonema augur* (GG), *Gomphonema pumilum* (GU), and *Halamphora montana* (HO).

During the wet season, TP, NO_3, and NH_4 were identified as the set of important environmental variables determining the distribution of diatom taxa among sites (**Figure 5**, Wet season). Axis 1 (46%) showed a nutrient gradient. The RDA triplot grouped some of Boye sites (B1, B2, B3, and B6) toward high NO_3-N and TP.

DISCUSSION

Quality of the Water Before, and After Joining the Wetlands

In Jimma, the natural riverine wetlands of the town receive streams which are considered as major carriers of the towns

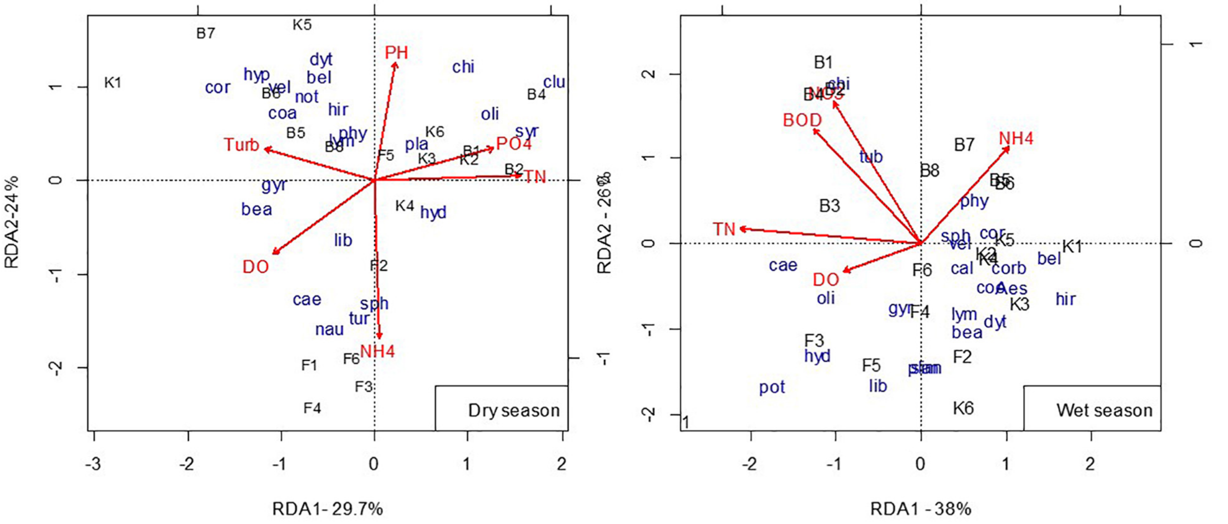

FIGURE 4 | Redundancy analysis triplot of macroinvertebrate taxa, environmental variables, and sites during the wet and dry seasons (see **Supplementary Table S5** for full names of taxa codes and **Supplementary Table S1** for the site codes). TUR, Turbidity; TN, Total Nitrogen; DO, Dissolved Oxygen; PO_4, Ortho phosphate; NH_4, Ammonium-Nitrogen; NO_3, Nitrate Nitrogen; BOD, Biological Oxygen Demand.

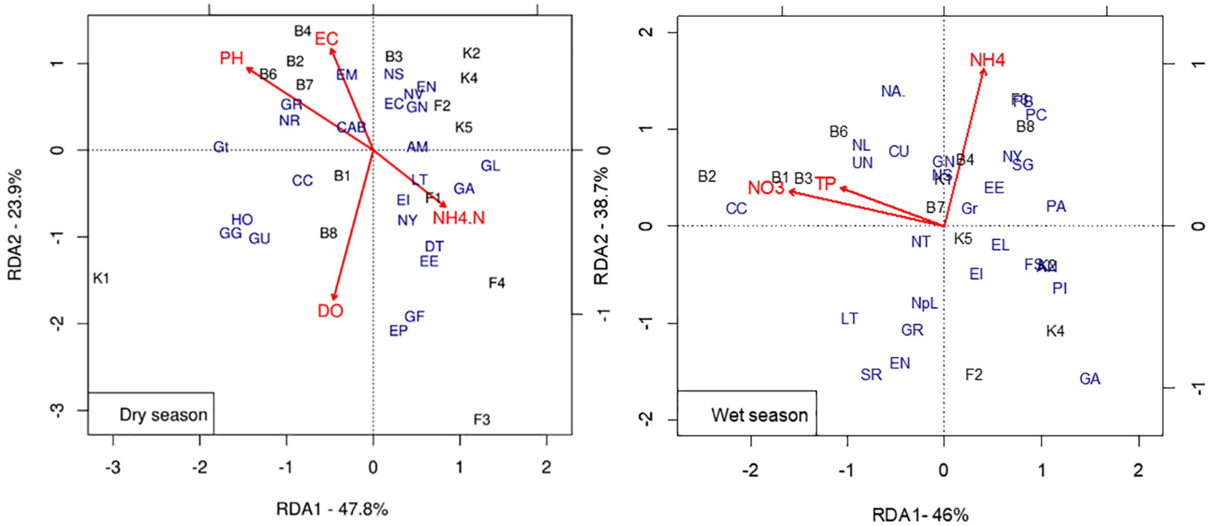

FIGURE 5 | Redundancy analysis triplot of diatom taxa, environmental variables, and sites (see **Supplementary Table S6** for full names of taxa codes and **Supplementary Table S1** for the site codes). DO, Dissolved Oxygen; EC, Electrical Conductivity; NH_4.N, Ammonium-Nitrogen; NO_3, Nitrate Nitrogen; TP, Total Phosphorus.

waste. These wetlands exhibited a potential to temporarily retain nutrients (TN, NH_4, TP, and PO_4) and organic pollutants (BOD). During the dry season, water quality improvement was observed by the significant reduction in concentration of TN and DIN, and a considerably lower NH_4 after passing through the wetland. Concerning phosphorus, a retention of TP and PO_4 was revealed from lowered concentrations in sites within the wetland and after passing through the wetland. These results are in line with a review done by Fisher and Acreman (2004) on the potential of natural wetlands to remove nutrients. Although there was a slight increase in the concentration of NO_3 in sites located within the wetlands, a significant reduction was observed in the effluent. The increased concentration within the wetland can be attributed to the conversion of ammonia to NO_3 or limited denitrification (Gómez et al., 2002). Unlike the dry season, no clear gradient was observed during the wet season.

The integrative response of biological indicators revealed the water purifying effect of the studied wetlands and their potential to support biodiversity. A considerable increase in taxa richness and Shannon's diversity of macroinvertebrates was observed in sites within the wetland and after passing through the wetland compared to those before joining the wetland. The relative abundance of filter collectors is among the recommended indices to assess ecological status of wetlands in Ethiopia (Mereta et al., 2012). The %FC and Ethbios index were also higher within the wetland. It can be associated with the reduced load of nutrients and organic pollutants after joining the wetlands. This agrees with the negative correlation of %FC with TP and PO_4, and Ethbios with TN (see **Supplementary Table S7**). A decrease in %FC with increasing level of organic pollution was also reported by Gebrehiwot et al. (2017) while evaluating the feeding interaction along a pollution gradient.

Lougheed et al. (2008) revealed a higher diatom taxa richness in sites with a relatively better quality than the most degraded sites. In this study, the higher diatom taxa richness and lower percent pollution tolerant taxa in sites after joining the wetland indicated water quality improvement. Shannon's diversity of diatoms also showed an increasing gradient within the wetlands and at the outlet. Additionally, negative correlation of diversity indices with DO and EC, and positive correlation of %PT with TP, TN, and DIN was observed (see **Supplementary Table S8**). Therefore, the observed positive gradient of the indices after joining the wetlands clearly indicates the wetlands' potential to purify water and to support biodiversity.

During the wet season, in areas of low flow rate, a higher water depth provides an increased attachment surface for diatoms by covering stone surfaces with water (Bojorge-García et al., 2014). Bojorge-García et al. (2014) reported a higher abundance of diatoms during the rainy season in tropical mountain streams of Mexico. Similarly, our finding indicated a higher abundance and richness of diatoms during the wet season. On the other hand, diversity indices of macroinvertebrates were lower in the wet season. Gebrehiwot et al. (2017) also indicated a similar finding. This might be due to habitat instability, resulted from increased runoff, which in turn drift off macroinvertebrates.

Purifying Efficiency Among Wetlands and Ecological Quality

The percent change of nutrients and organic pollutants differ among wetlands. This variation can be attributed to the difference in influent quality, and extent of catchment disturbance. Among wetlands, the concentration of nutrients and electrical conductivity were significantly higher in sites associated with Boye wetland than Fisho and Kitto wetland sites. This is because the streams associated with Boye wetland are the major carriers of Jimma town's liquid waste (Ambelu et al., 2013). The more polluted Boye wetland showed a higher TP reduction during the dry season. This can be due to the higher phosphorus input to Boye wetland from the streams flowing to it or anthropogenic pressure in the surrounding since its located in urban downstream. The wetlands nutrient retaining effect was not observed in wet season, rather there was more leaching of nutrients than reduction. This might be due to instability of sediments and habitats.

The biological indices reflect major ecological degradation in Boye wetland. High load of organic and inorganic pollutant makes the environment less favorable for sensitive taxa (Eppink et al., 2004). The highest percent of tolerant diatom taxa and the lowest Shannon's diversity, macroinvertebrate and diatom, was observed in Boye than the other two wetlands. This can be attributed to the heavily degraded incoming water to Boye. Compared to Boye wetland the other two wetlands, located in urban upstream, still have the capacity to sustain their ecological quality. This was indicated by the higher diversity and richness of the assessed bioindicators.

The Relation Among Environmental Gradient, Biota, and Sites

In this study, the RDA model reflected the dominance of macroinvertebrate taxa which are tolerant of heavy pollution, in the incoming streams of Boye (B1–B4) and characterized by a high load of nutrients (PO_4, TN, and NO_3) and organic matter (BOD). Beyene et al. (2009) reported the absence of macroinvertebrates in heavily polluted streams of Addis Ababa, Ethiopia. However, in this study, heavily polluted sites recorded a minimum of five. This discrepancy may be due to the difference in the type of pollution since the sites are located in a different land use type. The presence of moderately tolerant macroinvertebrate taxa in Boye sites after passing through the wetland indicated a relatively improved water quality. Most of Fisho and Kitto sites were dominated by moderately tolerant taxa. Highly tolerant taxa (Lakew and Moog, 2015) such as Oligochete were among the dominant during the wet season. During the dry season, the upstream of Kitto (K1) is characterized by a high level of DO and had a low level of organic pollution. This variation in macroinvertebrate communities among sites can be explained by the difference in habitat, and in the level of degradation. In general, the relation among macroinvertebrate community assemblage, environmental parameters, and sites, discriminate Boye wetland sites as the most degraded in both seasons. A previous study (Ambelu et al., 2013) also pointed out the presence of heavy degradation on this site.

Diatom taxa which are tolerant of high level of EC, e.g., *Craticula ambigua* (Alakananda et al., 2011) and heavy organic pollution and nutrients, e.g., *Navicula gregaria* and *Gomphonema parvulum* var. *parvulum* (Kelly et al., 1995; Gómez et al., 2008) were abundant in Boye sites along a high level of pH and EC. *Gomphonema parvulum* is among the taxa which are potential indicators of eutrophication (Bere and Mangadze, 2014). Less tolerant taxa, e.g., *Gomphonema augur* (Bauer et al., 2007) were found in Kitto upstream site (K1), which indicates good water quality. There was a homogenized distribution of highly tolerant, and moderately tolerant taxa during the wet season. This could result from the drifting effect of runoff since it is the major factor governing the seasonal variation in tropical wetlands ecosystem (Bellinger et al., 2006; Mitsch et al., 2010).

In indicating the water quality improvement and ecological quality, macroinvertebrates and diatoms, indicated a coherent response toward pollution gradient during the dry season. Similarly, a consistent response of these bioindicators was reported by Resende et al. (2010) in assessing water quality of the UI river, Portugal. Both bioindicators discriminated Boye site as the most ecologically degraded.

CONCLUSION AND RECOMMENDATION

In conclusion, this study proved the potential of natural riverine wetlands in Jimma, Ethiopia, to retain nutrients and organic pollutants. The gradient of nutrients, BOD, and DO before and after joining the wetlands showed retention of pollutants within the wetlands. Percent change of nutrients and organic pollutants varied among wetlands and between wet and dry seasons. During the wet season, a higher concentration of nutrients was observed within the wetland. However, the water quality was better (diluted) during the wet season. Macroinvertebrates and diatom metrics clearly indicated the water purifying effect of studied wetlands and their potential to support biodiversity. B1 and B3 of Boye were identified as severely degraded, whereas, K1 (Kitto upstream) was the only site with an intrinsic good ecological quality. In general, the integrated response of biota and environmental parameters discriminate Boye wetland sites as the most ecologically degraded. Hence, we conclude that, when the incoming water is heavily degraded, the retention of pollutants seriously affects the ecological quality of the wetlands themselves. Therefore, future integrated wetland management interventions should also target the incoming streams or rivers to reduce the nutrient and organic loading.

Therefore, this study suggested that when the influents are marginally polluted the natural riverine wetlands can serve as natural treatment systems without affecting their ecological quality. Simultaneous use of macroinvertebrates and diatoms along with environmental parameters is recommended to have a comprehensive information on water quality and ecological status of natural riverine wetlands. Future studies should include wetland macrophyte identification, and hydrological parameters, e.g., hydraulic retention time, to identify the major processes governing the nutrient removal.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

AS contributed in data collection, analysis, and manuscript writing. AA, AB, and LT contributed in designing the study, data analysis, and manuscript writing. IS contributed in manuscript writing.

FUNDING

This study was financially supported by VLIR-UOS and VUB (BAS42).

ACKNOWLEDGMENTS

We are grateful to Vlaamse Interuniversitaire Raad (VLIR-UOS) for funding the MSc study of Adey Seleshi and the Ph.D. project of Aymere Awoke Assayie; the Vrije Universiteit Brussel (VUB, BAS42), and Jimma University, Ethiopia for financial and logistic support.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00039/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 21 May 2020
doi: 10.3389/fenvs.2020.00049

A Multi-Scale, Participatory Approach to Developing a Protected Area Wetland Inventory in South Africa

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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *04 October 2019*
Accepted: *14 April 2020*
Published: *21 May 2020*

Citation:
Job N, Roux DJ, Bezuidenhout H and Cole NS (2020) A Multi-Scale, Participatory Approach to Developing a Protected Area Wetland Inventory in South Africa. Front. Environ. Sci. 8:49. doi: 10.3389/fenvs.2020.00049

Given limited time, staffing and specialist expertise, management of wetlands within biodiversity-rich protected areas of developing countries is often held back by a lack of information on the extent and nature of wetland resources. Rapid, realistic and effective wetland ecosystem assessment methods are needed to develop a baseline for monitoring that detects trends and guides management. For our case study national park, lack of available in-house wetland expertise stimulated a novel team approach to harness wide-ranging complementary and, ultimately, indispensable expertise, spanning several branches of the national park agency: park management and rangers, scientific services, and a unit responsible for invasive alien plant control and landscape restoration. Within a year, the team developed a sufficiently comprehensive inventory which captured the variation of wetlands present in Mountain Zebra National Park, South Africa. A total of 267 features were mapped, while 62 were visited in the field and assessed through rapid verification. Careful collation of existing data and imagery informed a catchment approach, an emphasis on wetland-landscape connectivity, and strategic targeting of a sub-set of important and representative sites deserving of targeted field assessment. The remaining wetlands not visited in the field were subject to geographic information system image interpretation. Overall, this resulted in a comprehensive overview assessment of the entire Park at multiple scales. The participatory approach followed here promotes integration of the findings of the study into park planning, management and rehabilitation. The process provides a potential template for scaling and adapting to similar work in other parks and other areas that have limited funding and capacity.

Keywords: wetland inventory, Mountain Zebra National Park, protected areas, participatory assessment, catchment and landscape approach, wetland management

INTRODUCTION

The mapping, classification, and description of wetlands and their associated biotic and abiotic features are vital steps in building a framework to understand, manage, rehabilitate and conserve these ecosystems (Finlayson and van der Valk, 1995; Finlayson et al., 1998; Zedler, 2000; SANParks, 2016). In developing countries, including within their biodiversity-rich protected areas, effective management of wetlands is hampered by a lack of information on the extent and nature of these ecosystems. In these countries, most nature reserve and national park management agencies have limited resources, including specialist expertise. This is also the case in the agencies mandated to support conservation at provincial and national level. For example, in South Africa only one out of nine provincial conservation agencies was found to support an adequate complement of dedicated aquatic scientists (Impson, 2016), and most institutions are experiencing declining funds (Van Deventer et al., 2019). Furthermore, wetland specialization is a relatively recent field of practice in South Africa so that, even where aquatic scientists are present, their expertise often does not include experience of wetlands. Also, wetlands are at the transition between terrestrial and aquatic habitats, and multi-disciplinary expertise is required to comprehensively assess and manage these systems.

In South Africa, assessment and management of wetlands is enabled and guided by three national-scale developments. First, the country has adopted a freshwater conservation target stating that at least 20% of each inland aquatic ecosystem type should be conserved (Roux et al., 2006). Second, classification and spatial mapping of wetlands made the extent of these ecosystems explicit (Ollis et al., 2013; Van Deventer et al., 2018, 2019). Third, a national planning exercise was conducted to identify strategic spatial priority areas for satisfying the 20% target. This resulted in 38% of South Africa's wetland areas being identified as Freshwater Ecosystem Priority Areas (FEPAs; Nel et al., 2011).

Notwithstanding the above advances, national-scale target setting and assessments do not automatically translate into local-scale implementation (Roux et al., 2016). Wetland validation and verification, and the involvement of wetland scientists and local managers, are essential but often overlooked. National-scale data, especially when derived from modeling or remote sensing, as was the case for South Africa's dataset, must be validated at scales relevant to management (Gouws et al., 2012; Mbona et al., 2015). At these scales, rapid and realistic wetland ecosystem assessment methods are needed to develop a wetland baseline, with comprehensive information about their distribution and with sufficiently accurate detail to allow management actions to be implemented.

Here we present an approach to map wetlands and validate national-scale wetland priorities (FEPAs) at the scale of a protected area, focusing on a national park as a case study. Although Mountain Zebra National Park (MZNP) is one of the smallest of South Africa's national parks (20,243 ha), it has all the features to exemplify what is involved in undertaking a wetland inventory, with limited resources. We present an overview of the approach and results of, to the best of our knowledge, the first wetland inventory for a national park in South Africa. Our approach includes wetland boundary delineation, wetland type classification and a preliminary wetland condition assessment. This involved a combination of office and field work, and the collaboration of a multidisciplinary team, including managers and field rangers. A key feature of the approach was identification of sub-catchments for the park and subsequent grouping and presentation of information associated with each sub-catchment. The inventory is presented as a geographic information system (GIS) data set and a report with maps to inform decision-making and provide a baseline for future monitoring, trends analysis and management of key issues. The step-by-step process could serve as a 'manual' for doing similar work in other protected areas.

MATERIALS AND METHODS

Study Area

Mountain Zebra National Park is one of the 19 national parks managed by South African National Parks (SANParks). It is situated in the Eastern Cape interior (**Figure 1**), extending northwards from the slopes of the Bankberg mountain range. The park ranges in altitude from 911 to 1,953 m amsl. The northern area of the park is located on a relatively undulating plateau, with moderate increases in altitude in an outwards direction to approximately 1,300 m.a.s.l. The altitude and topography of the park increase dramatically to the south, varying between 1,300 and 1,953 m.a.s.l, with a number of deeply incised river valleys (kloofs). Recorded average annual rainfall is 405 mm, and average daily temperatures range between 23.1 and 28.4°C in summer (September–March) and 16.2–22.7°C in winter (April–August) (Brown and Bezuidenhout, 2018). Minimum average temperature is 5.6°C in summer and 3.9°C in winter (Brown and Bezuidenhout, 2018). The southern mountainous peaks are exposed to frequent cloud cover and extreme temperature and moisture regimes, with local climate variations resulting in a number of microhabitats. The Bankberg forms a barrier to cold winter fronts, thus, a warmer climate is experienced in the sheltered valley below it, whilst frost and regular snowfall occurs on higher lying areas (Pond et al., 2002). Mucina et al. (2006) characterize the area as Karoo Escarpment Grassland (Gh1) and Eastern Cape Escarpment Thicket (AT13) vegetation types, within the Upper Karoo Bioregion. Bezuidenhout et al. (2015) have classified, mapped and described 13 plant communities for MZNP. They group these into three major landscapes, namely, mountain highlands rugged landscape; middle plateau rolling landscape; and valley bottomland undulating plains landscape (**Supplementary Figure S1**).

Mountain Zebra National Park was proclaimed in 1937 for the purpose of protecting a remnant population of the Cape mountain zebra (Van Riet, 1977; Van der Walt, 1980). To make the park both ecologically and financially more viable, it was expanded in the late 1990s from 6,536 to 20,243 ha through incorporating private land. This expanded the scope of MZNP from being a "species park" to also conserving the biodiversity of the region, including charismatic species such as cheetah, brown

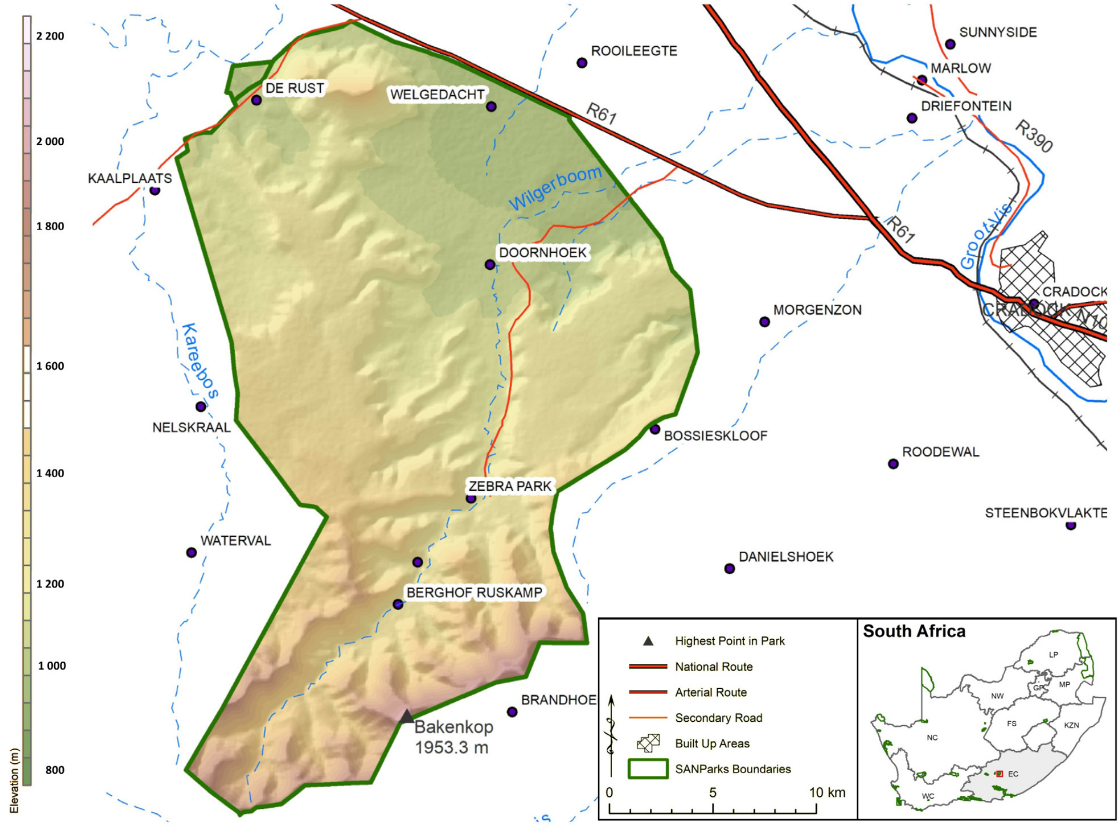

FIGURE 1 | Location of Mountain Zebra National Park.

hyena, Cape buffalo and lion, and a diverse range of ecosystems and landscapes (SANParks, 2016).

Sub-Catchment Management Units

Water Management Areas (WMA) have been defined in the South African National Water Act (Act 36 of 1988) and delineated throughout South Africa as primary units for catchment management. These areas are extensive and encompass many main stem rivers and thousands of tributary streams. Mountain Zebra National Park falls within the Fish to Tsitsikamma WMA and Fish sub-WMA. Sub-WMAs are further sub-divided into quaternary catchments (average area of 20,000 ha or more, **Table 1**), and, in 2011, a finer sub-division of quaternary catchments was undertaken producing quinary catchments as part of the NFEPA project (Nel et al., 2011; **Table 1** and **Figure 2**). Quinary catchments in MZNP range between 15,000 and 4,500 ha (**Table 1**) and where necessary, 2 or 3 are grouped together to represent the contributing area for only one river or stream per group, which makes them best suited for hydrological management at a local scale. Although these management units exist in the country, it is rare, nation-wide, for managers to organize their management holistically according to sub-catchments. Applying the quinary catchment as the base unit for the wetland assessment strongly links the wetland to its associated terrestrial catchment landscape, where many processes driving wetland hydrology are initiated. It also develops a feel for the catchment landscape, especially of the variation in wetland types present, and allows impacts to be identified and contextualized at a catchment scale, so that relationships may be better understood.

Convening a Multi-Disciplinary Team

The practice of wetland science is multi-disciplinary, encompassing but not limited to: GIS, soil science, vegetation ecology, hydrology, and aquatic science. South African National Parks supports most of these skills within their Conservation Services Department, but a focus on inland wetlands was a relatively new area of exploration for this agency. The process of developing a wetland inventory for MZNP, therefore, involved development of wetland-specific understanding and sharing of knowledge across multiple sets of expertise. One external wetland specialist and more than 15 SANParks staff including park management and rangers, scientific services and a unit responsible for invasive alien plant control and landscape restoration, participated in and contributed to the inventory. Apart from assembling an in-house team able to undertake wetland inventory, a further goal was to facilitate appreciation of wetlands as biodiversity features, and an understanding of their ecological functions and sensitivities. In this regard, it was considered vital to include additional park staff, such as rangers and park managers, from the outset, not only once there was a

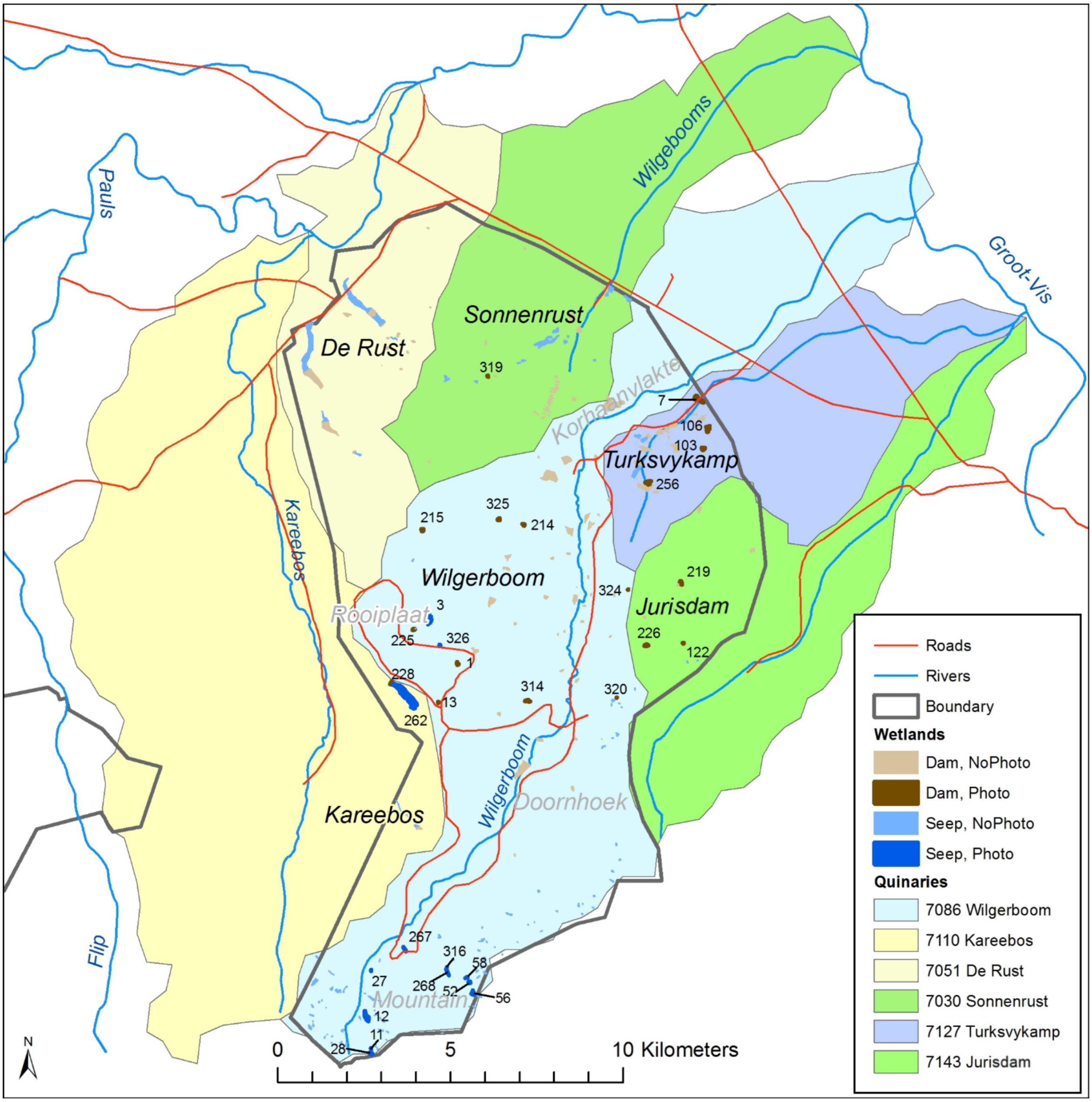

FIGURE 2 | Mountain Zebra National Park sub-catchments.

completed product. This allowed their extensive knowledge of the Park and landscape processes to be incorporated into the wetland assessment.

Wetland Mapping

Steps 1 to 9 are in visualised in **Figure 3**. Step 1. Compile existing (secondary) data relevant to the study area. Data was compiled as comprehensively as possible from multiple sources, to capture and build upon existing information and knowledge, scanning for any mention of rivers, wetlands, riparian habitat, dams, or water. **Table 2** lists information supporting the GIS interpretation and illustrates the multiple useful ways data was contributed and verified by park staff over time through their various work programs, none of which were primarily focused on wetlands. In MZNP, the recent park-wide description and mapping of vegetation and habitat landscape units was a significant input (Bezuidenhout et al., 2015; **Table 3** and **Supplementary Figure S1**).

Step 2. Apply and improve data to locate wetlands and their boundary. The information collated from park staff was collected as point data (latitude and longitude location data, visualized as points in GIS) and required an extra step to turn it into spatial

TABLE 1 | Mountain Zebra National Park catchments.

WMA	**Fish to Tsitsikamma**					
Sub-WMA	**Fish**					
Quaternary ID	**Q30B**		**Q30C**	**Q30D**		
Quinary ID	7110 (B)	7051 (C)	7030 (D)	7086 (A)	7127 (E)	7143 (F)
Name	Kareebos	De Rust	Sonnerust	Wilgerboom	Turksvykamp	Jurisdam
Total area (ha)	15,121	5,280	6,890	13,923	4,569	5,736
Area in MZNP	1,128 (7%)	2,122 (40%)	3,153 (46%)	11,236 (81%)	1,263 (27%)	1,612 (28%)

*The A-F in the 'Quinary ID' row refer to labels used in **Figure 2**.*

TABLE 2 | Data sources informing the final wetland map of MZNP.

Source layer	**Description**	**#**
	Secondary data	
NFEPA Wetlands	Wetland dataset from the National Freshwater Priority Areas (NFEPA) project	101
WaterPoints Natural/Artificial	Provided by Regional Ecologist, based on water points on park's management map	171
	Primary data	
Wetland Pins (Draft map 1 location)	Potential wetland areas (points) identified on GIS by specialist and Manager	205
Wetland Points Confirmed	28–29 April 2015; field confirmation by Biodiversity Social Projects and an Environmental Monitor of 13 wetland pins	13 validated
Draft map 2 (location, extent and type)	First version GIS polygon map	263
Field visit #1	17–19 March 2015; team of 15 SANParks staff (including park management, Scientific Services and Biodiversity Social Projects); exploratory visit that helped with inter-group communication and general orientation	6 validated
Draft map 3 (location, extent and type)	Second version, revised GIS polygon map	317
Field visit #2	16–19 November 2015; 7 SANParks staff plus wetland specialist; ground-truthing of GIS-derived inventory for selected sites	62 validated
Draft map 4-6 (location, extent and type)	Final revised GIS polygon map – 139 artificial (includes modified springs), 7 unknown, 28 riparian, 100 wetland (seep wetlands)	267

data, that is, a map of the wetland area. Thus, a first review and improvement of wetland location and boundary accuracy of collated wetland mapping information was undertaken, and additional wetlands were then identified through aerial image interpretation and mapping in GIS. This was undertaken in ArcMap 10.3 and Quantum GIS (QGIS) using a combination of SPOT 5 imagery, Google Earth satellite imagery, 1: 10,000 aerial images, a digital elevation model prepared for MZNP, and 20 m contour and 1:50,000 river lines both obtained from the Chief Directorate: Survey and Mapping. The 1:50,000 rivers and contours layers help identify stream lines and landscape locations where potential wetlands are typically located. Wetlands were digitized at different scales, depending on their visibility and size. The optimal scale (being able to zoom in as far as possible without the image being blurry) ranged between 1: 2,000 and 1: 3,000. This scale range is most useful to locate and identify a wetland and its type. However, digitizing the final wetland boundary required one to zoom in as close as 1: 400.

Step 3. Review and clean data. This step focused on a review of the mapped boundaries over aerial imagery, to ensure none were artificial, as most dams could be recognized through GIS image interpretation. All dams (artificially altered wetlands, as well as dams created in historical non-wetland areas) were identified through GIS image interpretation prior to going in the field, to focus the field time on natural systems. This allowed for potential wetlands in the remoter areas of the park to be identified for further investigation, as well as preparing fieldtrips more effectively.

Step 4. Wetland typing. Typing of freshwater ecosystems according to broadly similar hydrologic processes (the way in which water moves into, through and out of the wetland systems) and geomorphic factors (such as the position of the wetland in the landscape, landscape shape and likely associated active processes) for this study followed the hydrogeomorphic (HGM) classification developed for South Africa by Ollis et al. (2013), adapted from Brinson (1993). These wetland HGM types include floodplain, channeled and unchannelled valley-bottom wetlands, seeps, depressions, and wetland flats. Creating a digital elevation model in GIS and assigning of certain attributes to the wetlands such as slope (e.g., seep wetlands), landscape position and shape (e.g., depression wetlands in closed contour areas) assisted with GIS image interpretation and supported preliminary allocation of wetland HGM type on GIS ahead of going into the field.

Step 5: Fieldwork supporting tools. A mapbook was created with a reference map for orientation and overview of the full study area. The overview map was overlain with grids, each

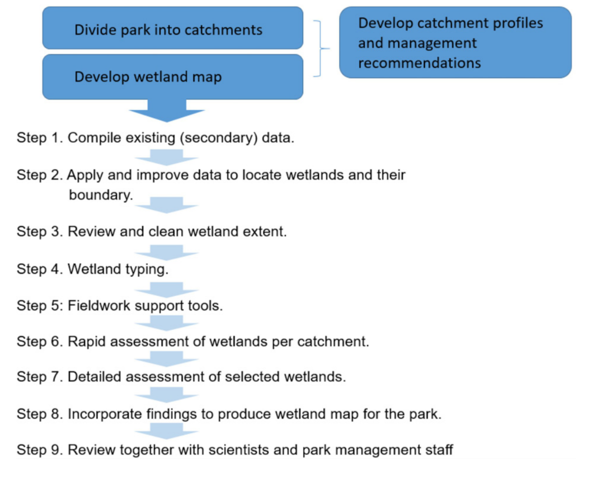

FIGURE 3 | Flow diagram of wetland inventory approach.

grid labelled with a unique id. Detailed "zoomed in" maps were prepared and printed out for in-field use, one for each grid. A field datasheet was prepared and printed out for hand-written note-taking in the field. The field team also tested the utility of different mobile devices, including iPads, cell phones, and a variety of hand-held GPS devices including Trimble Juno 3B. ESRI's ArcMap10x was used to create maps and ArcGIS Collector used to develop sequences for infield data collection. The set-up of predetermined coded values to choose from ensured the data capturer adhered to pre-determined naming conventions. These were loaded onto those handheld devices running Arcpad or ArcGIS Mobile Software.

Step 6. Rapid assessment of entire catchment. For MZNP, the aim of achieving a comprehensive inventory with limited budget and time was achieved in the field component through a combination of detailed field assessment (high confidence results) for select, representative, wetlands and rapid assessment (moderate to high confidence results) for as many more wetlands as it was possible to view within a two or three-day field trip (between 16 and 18 November 2015). The efficiency with which wetlands were visited and assessed benefited from the participation of rangers with long-term and extensive field experience of the park. In order to cover large areas of the park, and taking into consideration the relative homogeneity within wetland and across wetland types in the park, the rapid assessment was preferred for the majority of field work, including a rapid walk through, or in some cases, a drive past, and recording of key wetland characteristics. This included checking wetland presence and key characteristics or the presence of an artificial system against the hardcopy map, and capturing data into handheld GPS's. The rapid assessment was conducted in a catchment at a time as much

TABLE 3 | Summary of landscape and plant communities of MZNP (Bezuidenhout et al., 2015).

Mountain highlands rugged landscape (B) and plant communities
Rocky outcrops cover 60–80% of the area. The steep midslopes are the most prominent topographical unit in this mountainous landscape, dominated by rock, while the Glenrosa soil form is subdominant (Soil Classification Working Group, 1991). The geology of this landscape consists of dolerite with mudstone, shale and sandstone of the Balfour Formation, Beaufort Group of the Karoo Super group (Land Type Survey Staff, 2004). Closely associated with tall (1 m), closed canopy cover grassland and sparsely distributed shrubs
B1 *Eragrostis lehmanniana – Eragrostis curvula* Grassland
B2 *Merxmuellera disticha – Euryops annuus* Grassland
B3 *Merxmuellera disticha – Felicia filifolia* Grassland
B4 *Searsia lucida – Diospyros lycioides* Woodland
Middle plateau rolling landscape (M) and plant communities
Duplex soils dominate, such as Swartland and Valsrivier soil forms. Plains are dominated by plateau midslopes, but also include steep midslope and footslope topographical units. The geology of this landscape is mudstone, shale and sandstone of the Balfour Formation, Beaufort Group of the Karoo Supergroup (Land Type Survey Staff, 2004). This landscape, of which the plateaux of Rooiplaats and Jurisdam are the most prominent areas, is dominated by medium tall (0.3–0.8 m), open to closed canopy cover grassland. Rocky outcrops are dominated by dwarf shrubs and other woody plant species
M1 *Carissa macrocarpa – Rhigozum obovatum* Shrubland
M2 *Pentzia globosa – Searsia longispina* Shrubland
M3 *Enneapogon scoparius – Vachellia karroo* Woodland
M4 *Searsia lucida – Buddleja glomerata* Shrubland
Valley bottomland undulating plains landscape (V) and plant communities
Pedologically young landscapes, predominantly rocky and alluvial. Lime regularly occurs in upland and valley-bottom soils (Land Type Survey Staff, 2004). Soil forms that epitomize this land type are Glenrosa and Oakleaf. The geology of this landscape consists of mudstone, shale and sandstone of the Beaufort Group of the Karoo Sequence with rare dolerite intrusions (Land Type Survey Staff, 2004). Two topographical units are prominent in this terraced landscape, namely the valley bottomlands and drainage lines which include the Wilgerboom River. The landscape is dominated by relatively tall (3–5 m) closed to open canopy cover woodland whereas grass species are less conspicuous and mostly dominated by annual grass species with a low canopy cover (<35%) and low height (<0.5 m)
V1 *Pentzia incana – Eragrostis lehmanniana* Forbland
V2 *Sporobolus africanus – Enneapogon scoparius* Grassland
V3 *Pentzia globosa – Eragrostis obtusa* Forbland
V4 *Aristida adscensionis – Chloris virgata* Grassland
V5 *Lycium oxycarpum – Vachellia karroo* Woodland

as the road network and other access would allow. Having the already prepared maps and other handheld tools with annotations of wetland type and other characteristics greatly facilitated the rapid survey, allowing validation, as well as new additional information to be collected, and allowing ground to be covered more rapidly.

Step 7. Detailed assessment of selected sites. A more detailed assessment was applied to a sub-set of wetlands considered to be representative of the wetland types present as identified during the GIS image interpretation. This involved an assessment of the entire wetland, noting vegetation, soil and hydrology characteristics. The goal was a species list, as well as identification of dominant or indicator species, and a description of soil and hydrology per habitat unit or zone if there were multiple. The approach to assessing wetland condition followed that of WET-Health (Macfarlane et al., 2009) and included assigning a wetland impact score on a scale of 0 (unimpacted) to 10 (critically altered) based on estimated change from the historical natural condition. There are many, complex factors which affect wetland condition, not all of which may be visible during a once-off field visit, particularly where only a part of the wetland is visited. For this reason, the field datasheet stipulated only a sub-set of specific issues for the rapidly assessment, to allow results to be nationally consistent. This focused on two wetland components, namely hydrology and vegetation.

Step 8. Incorporate findings and adjust mapping on GIS. The high confidence site assessments and understanding gained from the field trip informed GIS extrapolation of information to any areas missed in the remainder of each sub-catchment, especially for inaccessible areas. This led to adjustments of wetland spatial extent and designation of wetland HGM types, and the deleting of a number of polygons. The final set of GIS attributes for each of the mapped wetlands were assigned High, Moderate or Low levels of confidence. The confidence score was applied separately to wetland HGM type as well as spatial boundary. High confidence status was afforded to mapped wetlands that were ground-truthed and reviewed by the team. Moderate confidence wetlands were reviewed by the team, but not ground-truthed. Low confidence wetlands were mapped at a GIS image interpretation level, but not ground-truthed, implying uncertainty and a need to investigate further. Managers and other park staff were consulted for their insights during this stage, and to discuss monitoring and management needs.

The wetland inventory of MZNP emerged from several cycles of GIS image interpretation mapping, followed by selected field investigations, and extensive GIS image interpretation follow-ups. First was an investment in GIS preparation and data collation, aiming to comprehensively cover the study area and to delineate sub-catchments, amounting to approximately 40% of project time. Secondly, a combination of field ground-truthing of questions arising from GIS preparation and selected wetlands representing the anticipated different types in each catchment of the study area, as well as a more rapid visit through the remainder of each catchment amounted to approximately 20% of project time. Finally, GIS image interpretation follow-up to consolidate and apply the findings to the full study area and review the findings amongst the team members, other experts and managers. This amounted to approximately 40% of project time.

Step 9. Review together with colleagues and managers, supported by new map products.

RESULTS AND DISCUSSION

The Real Wetlands of Mountain Zebra National Park

The two key informant secondary datasets for wetland location during Step 1 were the national (NFEPA) dataset and the dataset of water points for game. Our review of the 101 national (NFEPA) mapped wetland features found that 49 of these polygons were non-wetland and 52 were artificial (dams). These findings were validated in the field during Step 6. Thus no natural wetlands were mapped by the national-scale NFEPA wetland layer for MZNP. The water point dataset added a further 119 points, to a total of 171.

The first, and all subsequent, rounds of mapping for MZNP undertaken during Steps 2–5, and Step 8, were spatially comprehensive, with a view to covering the entire park. During the first round of GIS imagery interpretation and digitizing (Step 2), 34 new wetlands were mapped (**Table 2**, GIS map 1 total of 205). Wetland location mapping in GIS was reviewed several times, with 58 new wetlands mapped in draft 2 (**Table 2**, GIS map 2, total of 263) and 54 in draft 3. This amounted to 317 polygons mapped prior to field validation.

During Steps 6 and 7 (field validation), several mapped features were confirmed during the field visit to be artificial (dams, quarries, watering troughs, reservoirs) bringing the total number of dams and water points to 139, 50 mapped features were deleted once it was confirmed in the field they were neither wetland nor dam, 28 were assigned to be stream channel or riparian areas and 7 were designated “unknown” due to inaccessibility. Only 100 were validated or extrapolated to be natural seep wetlands (**Figure 2**), ranging in size from 2 ha to approximately 0.06 ha. The 100 seep wetlands cover a total area of 261 ha or 1.2% of the surface area of MZNP. Representative photographs of the range of freshwater ecosystems within MZNP are included in **Supplementary Plate 1**.

There was a significant learning and, hence, change in the type and number of wetland HGM types mapped during the first and second GIS image interpretation exercises, for example two seeps were mapped in the first round and this was amended to 100 in the final count. This was based on feedback from the rapid field visit and review with the field team, including a wetland ecologist.

Catchment Units Support Management

Dividing the national park into hydrologic management units according to sub-catchments was a new management approach for the park (**Box 1**). This was approached together with managers and rangers to ensure that descriptive and familiar local names were matched with the best fit hydrological boundary. Sub-catchment names were ultimately based on a combination of the existing division of MZNP into management sections combined with the names of the main rivers in each catchment

BOX 1 | Wilgerboom sub-catchment profile.

Landscape	Mountain highlands rugged landscape
	Middle plateau rolling landscape
	Valley bottomland undulating plains landscape
Landscape vegetation types	B1; B2, B3; B4; D1; G1; M1; M2; M3; M4; O1; V1; V3; V4; V5
Altitude	1000–1960 masl
Mapped aquatic ecosystems	2 springs, 47 dams, 2 riparian; 8 field visited
Mapped wetland ecosystems	98 seep wetlands; 7 field visited

Catchment characteristics: The sub-catchment was divided into an upper (Mountain), middle (Doornhoek) and lower (Korhaanvlakte) section, due to noticeably different plant communities and moisture regimes with different management requirements. Evidence of the fractured nature of the rock and flows of water from the rock can be seen in the prevalent white streaking on many outcrops and areas of surface bedrock, evidence of calcium carbonate due to water that has moved through the lenses of limestone said to be present within the sandstone (Toerien, 1972). Shelves of protruding sandstone are evident in the upper catchment. Wetland characteristics: The 98 mapped seep wetlands occur exclusively within the higher altitude, mountainous areas of the park, associated with higher rainfall. Seep wetlands are typically dominated by subsurface flows which generate saturated soils, with limited to no ponded water on the wetland surface. The seep wetlands can be broadly grouped into those forming on the high-lying rocky shelves, and those on long side slopes below the outcrops. These rocky outcrops act as a geological control, giving rise to several small pockets of wetland upslope of the shelf, described elsewhere by Le Roux et al. (2015). There is a notable prevalence of springs, resulting from the prevailing geology. The wetlands support a diverse range of sedges and herbaceous species, including *Eleocharis dregeanus, Juncus oxycarpus, Juncus capensis, Mentha longifolia, Lobelia erinus*, *Juncus effuses, Crassula natans*. The slope is moderate to steep. Wetland soils are relatively shallow (<0.3–0.5 m) and the water ponds on bedrock leading these wetlands to be permanently saturated, evidenced by the presence of gray to gley colored soil with high clay-content (>30%).

The long slopes within the mid-section of the Wilgerboom catchment support a second type of seep which is typically seasonally saturated and is located below the high-lying rocky outcrops, often extending down to the stream valley. These wetlands receive their water via a different mechanism to those on the bedrock shelves, rather the water flows laterally as shallow interflow within soils which overlie less permeable horizons horizons (e.g., sandier soils over soils with higher clay content) within the surrounding hillslope duplex soils and also with a second, deeper flow path at the interface of the soil and underlying bedrock (Van Tol et al., 2013; Le Roux et al., 2015; Job and Le Roux,2018).

Management recommendations: Of the four seep wetlands assessed in detail in the field in the upper section, namely Wetlands 11, 12, 28, and 56 (**Figure 2**), all showed signs of trampling and grazing, evidence of the use of the wetlands by game. In the wettest seeps, "potholing" or deep hoof prints were noted, which could lead to erosion knick-points in these very steeply sloping systems. This was likely a contributing factor in Wetlands 12 and 28, two seeps which appear to have become desiccated following extensive erosion and an associated lowering of the water. Management recommendations include close observation of trampled areas within wetlands for signs of erosion. Grazing pressure could be managed for less vulnerable times of the year. This a supported by the current fire plan of the park, namely (1) *lassaiz faire* "natural" fire regime on the mountainous regions of the park, (2) patch mosaic fire regime for removal of moribund material, and (3) burning of firebreaks for safety and security. Monitoring (mapping and record keeping) of fires in the park needs to be improved and co-ordinated.

Several seep wetlands have been impacted by roads crossing through them with subsequent formation of erosion gullies, leading to drying out of sections of the wetland (Wetland 56, **Figure 2**). The negative effect of roads cutting through the seep wetlands of the upper catchment, a legacy of previous farming practices as well as current access needs to patrol the fenceline and firebreaks, warrants further assessment, followed by the development of appropriate rehabilitation and maintenance measures and guidance on the design and placement of any new roads.

(**Figure 2**). Six sub-catchments (quinary catchments) were identified (**Figure 2**).

With the exception of Kareebos sub-catchment, which lies largely outside of the park, and Jurisdam sub-catchment of which only 50% of the headwaters are protected, the park protects the entire headwaters of the remaining four (quinary) sub-catchments and, thus, plays a significant local role with respect to freshwater conservation, despite not being identified as national freshwater priority (FEPA) catchments. Most sub-catchments are 3,000 ha or less (**Table 3**), while Wilgerboom catchment provides the most significant conservation contribution, with approximately 80% of this sub-catchment (11,236 ha) falling within MZNP. This sub-catchment supports 98 of the 100 seep wetlands mapped for the park, and is, therefore, an important catchment from the perspective of wetland management. The seeps are largely in a good ecological condition and the park potentially makes a significant contribution to the conservation of these wetland ecosystem types at the regional and national scale.

In our study, catchments units were used as basis for formulating wetland-relevant management recommendations (SANParks, 2016). For example, the upper Wilgerboom catchment (mountainous south) was noted to support grasses predominantly unpalatable to wildlife, which limits herbivory and helps protect wetland habitat. To relieve pressure from the drier northern plains, however, a management strategy to attract game into these areas has been to burn the grass on the hilltop and slopes (Novellie, 1990). The early regrowth is more palatable and more animals are then likely to make use of this food source. However, problems associated with burning wetland areas for grazing include increased numbers of grazers on the wetland areas, with associated increased trampling and compaction of soil. On the other hand, the exclusion of fire from mountainous areas may result in an increase in the densification of woody species (Brown, 1997). It was therefore advised that fire management practices for MZNP should aim to imitate natural regimes and processes (Bezuidenhout et al., 2016).

CONCLUSION

National-scale data can limit local-scale implementation if not validated and verified on the ground. Working at the local scale enables quality checking and feedback on national data. Results from this study are in stark contrast to the national depiction of wetland extent and richness, highlighting the essential role of wetland scientists and local managers to complement the efficiencies and reach of the top-down national approach. No wetland in the park was identified as a national wetland FEPA (Nel et al., 2011) and none of the seeps that occur along the slopes in the south of the park are included on the national-scale FEPA maps. This contradiction (between national-scale data and local reality) highlights the need for field-based mapping of wetlands in the park and for feeding the validated wetland information back to the South African National Biodiversity Institute (SANBI) for refinement of national wetland data. This has indeed happened, and subsequent refinement of national-scale wetland mapping in South Africa has benefited from the local-scale validation that took place in our study as well as elsewhere (Van Deventer et al., 2020).

Often passed over as time-consuming, local wetland ecosystem assessments are essential to develop a wetland baseline for any protected area, with distribution information and sufficiently accurate detail to allow understanding of what drives local wetland type functioning for management actions to be implemented. To achieve a rapid, realistic and effective wetland inventory within a reasonable timespan, the method developed for this study focused on collecting less in-depth data, but on all of the wetlands of the study area. This comprehensive approach facilitates an understanding of the variation in wetland types and impacts present in the park. The approach includes a significant time investment in GIS image interpretation, considered essential preparation before going into the field as it provides a rapid and comprehensive cover of an area. At this scale, the majority of wetlands can be identified and their boundaries roughly mapped through interpretation of aerial imagery. In the case of MZNP, even though it is one of the smaller National Parks, the landscape is rugged, ease of movement for fieldwork is constrained by the potential presence of dangerous wildlife, and the field team was only able to visit a small sub-set of the total wetlands over approximately eight field days. It was found to be most efficient to map as many wetlands as possible ahead of the field work, and also to allocate them a draft GIS-assessed wetland type, to allow the field team to most efficiently plan which locations to visit in the field, and to highlight an initial set of uncertainties requiring resolution through field investigation. Thus, this paper supports the case for a mixed methodology of image interpretation and field validation (Rebelo et al., 2017) to achieve a high confidence inventory for an extensive area. In addition, "rapid" and "detailed" (**Figure 2**) approaches are combined to deliver a multi-level approach (Nestlerode et al., 2014) in order to comprehensively cover the full park area.

The identification of sub-catchment units is an important component of the approach and promotes management from a hydrological perspective. Working to map the complete set of wetlands in each sub-catchment at a time facilitates a feel for the catchment landscape and allows impacts originating from this associated area to be identified and contextualized, so that relationships may be better understood and managed. Lack of available in-house wetland expertise stimulated a novel team approach which harnessed wide-ranging complementary expertise. The insights of rangers, managers and the mix of skillsets present during the fieldtrip enabled understanding of these previously under-studied ecosystems to be aligned with the existing landscape unit approach to management in MZNP. The existing approach of the park to manage according to landscape unit type (plant community, soils, climate) (Van der Merwe et al., 2015) provided a strong departure point. Wetlands are a result of their catchment landscape, resulting from the prevailing geology, topography, soil, and climate and, thus, align well with this management approach.

The approach of convening a multi-disciplinary team also promotes integrated implementation of the findings into park planning, management, and rehabilitation. We believe that our approach provides a potential template for rolling out similar work in other parks and other areas that have limited funding and capacity.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

The corresponding author prepared the manuscript, with contributions and review from all authors. All authors participated in field work associated with the study.

ACKNOWLEDGMENTS

We thank South African National Parks and the South African National Biodiversity Institute for funding and support of this research, as well as Lucky Ramalala for assistance in the early stages of the GIS process and Abel Matsapula for assistance with the maps.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00049/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 22 May 2020
doi: 10.3389/fenvs.2020.00058

Prediction of Wetland Hydrogeomorphic Type Using Morphometrics and Landscape Characteristics

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Specialty section:
This article was submitted to
Freshwater Science,
a section of the journal
Frontiers in Environmental Science

Received: 30 August 2019
Accepted: 28 April 2020
Published: 22 May 2020

Citation:
Rivers-Moore NA, Kotze DC, Job N and Mohanlal S (2020) Prediction of Wetland Hydrogeomorphic Type Using Morphometrics and Landscape Characteristics. Front. Environ. Sci. 8:58. doi: 10.3389/fenvs.2020.00058

Accurate spatial maps of wetlands are critical for regional conservation and rehabilitation assessments, yet this often remains an elusive target. Such maps ideally provide information on wetland occurrence and extent, hydrogeomorphic (HGM) type, and ecological condition/level of degradation. All three elements are needed to provide ancillary layers to support mapping from remote imagery and ground-truthing. Knowledge of HGM types is particularly important, because different types show different levels of sensitivity to degradation, and modeling accuracy for occurrence. Here, we develop and test a simple approach for predicting the most likely HGM type for mapped yet unattributed wetland polygons. We used a dataset of some 11,500 wetland polygons attributed by HGM types (floodplain, depression, seep, channeled, and un-channeled valley-bottom) from the Western Cape Province in South Africa. Polygons were attributed and described in terms of nine landscape metrics, at a sub-catchment scale. Using a combination of box-and-whisker plots and PCA, we identified four variables (groundwater depth, relief ratio, slope, and elevation) as being the most important variables in differentiating HGM types. We divided the data into equal parts for training and testing of a simple Bayesian network model. Model validation included field assessments. HGM types were most sensitive to elevation. Model predication was good, with error rates of only 32%. We conclude that this is a useful technique that can be widely applied using readily available data, for rapid classification of HGM types at a regional scale.

Keywords: Bayesian network, classification, South Africa, Western Cape, probability, principal components analysis

INTRODUCTION

One of the means of categorizing wetlands is according to hydrogeomorphic (HGM) type, which is defined by geomorphic setting (e.g., hillslope or valley-bottom), water source (e.g., surface water dominated or sub-surface water dominated) and pattern of water flow through the wetland unit (diffuse or channeled) (Brinson, 1993; Ollis et al., 2013). Given the fact that HGM types are defined in terms of key driving process that underlie wetlands (Brinson, 1993) they provide a useful means of inferring ecosystem functioning and supply of ecosystem services (Euliss et al., 2013) as well as a means of delimiting broad response units for ecological condition assessments (Kotze et al., 2012).

It has been noted further how HGM types differ in terms of degradation patterns (Rivers-Moore and Cowden, 2012) and vulnerabilities (Kotze, 2011). Therefore, classifying wetlands according to HGM type has a potentially useful contribution to make toward assessing and promoting the sustainable use of wetlands, particularly at a broad catchment/landscape scale.

While data on wetland extent, HGM type, and ecological condition are increasingly recognized as important for global- and regional-scale (province, state, county, or catchment) wetland assessments, methods, and studies on these approaches are limited worldwide (Guidugli-Cook et al., 2017). Historically, wetlands have been iteratively mapped and typed using a combination of field assessments and interpretation of aerial photographs. This is not only a labor intensive process, but typically leaves large swathes of landscape under-mapped. Consequently, there is an increasingly widespread application of satellite imagery data for wetland inventory and mapping; although currently used techniques have recognized limitations for detecting some types of wetlands (see for example Davidson et al., 2018). Whereas, national wetland inventories are not available for many parts of the world, where these do exist, there are often concerns about accuracy, or data deficiency such as for cases when wetland polygons have no attributes. Large discrepancies in concurrence between national inventories and field observations of wetlands (Guidugli-Cook et al., 2017) raises concerns about the reliable use of national datasets when scrutinized at a regional or local scale.

In South Africa there are tens of thousands of wetlands covering 2.6 million hectares (van Deventer et al., 2020), and therefore to type all of these wetlands manually would require considerable resources. If reliable automated method/s using model/s can be developed for identifying HGM type, they offer the means of typing wetlands at a fraction of the cost of doing so manually.

However, to date, attempts to automate the identification of HGM type have met with very limited success, and in two test areas in the Western Cape, the automated HGM types yielded a very low level of congruency with the field-verified HGM types (van Deventer et al., 2016). For previous studies on modeling HGM type for South Africa, the analysis was based on a 90 m digital elevation model (DEM) and on the interim step of generating landform classes (van Deventer et al., 2016). While adequate for representing the range of landforms at a country-wide scale, there was an under-estimation of slope and an over-estimation of valley floors, and an overall accuracy of 43% was estimated for prediction of wetland HGM type which is not sufficient for decision making at the local scale (van Deventer et al., 2014). Nevertheless, fundamental to setting conservation targets for landscape features such as wetlands, as well as prioritizing wetland systems, for example, for rehabilitation, is a sound spatial layer of wetland occurrence (location and extent) that includes information on wetland hydrogeomorphic type and ecological condition. Here, we recognize that spatial wetland ancillary data should be developed in a logical sequence, beginning with occurrence and extent, followed by hydrogeomorphic (HGM) type, and then ecological condition. We include ecological condition as the final step based on catchment-scale ecological condition models that showed that different HGM types respond to different predictor variables; for example, elevation was the best predictor of floodplain ecological condition, while population density was a significant predictor of seep ecological condition (Rivers-Moore and Cowden, 2012). Given the variable nature of these wetland parameters within the landscape, it is more pragmatic to assign degrees of probability rather than absolute classifications to mapped wetlands. In other words, ancillary data layers will be able to provide probability values for occurrence, type, and ecological condition, from which wetland practitioners will be able to make statements such as "at this location, there is an 85% probability of a wetland occurring, which is five times more likely to be a seep than a floodplain, and there is a 70% probability that it is in a degraded state." Here, the ecological condition of a wetland refers to present condition relative to an un-impacted reference condition which shows little or no influence of human actions (Anderson, 1991). In southern Africa, owing to limited availability of data on biological response indicators, the assessment of ecological condition generally requires a strong reliance on stressor-based indicators, in particular relating to land-cover and land-use in the wetland and its influent catchment (Kotze et al., 2012). The assessment method developed by Kotze et al. (2012) provides standardized metrics for assessing ecological condition of wetlands in South Africa, and is designed to account as far as possible for the differential responses of HGM types to specific stressors.

It is therefore logical that landscape-level predictive models, based on "soft" classification techniques, should be used to complement traditional approaches to wetland mapping. In South Africa, logistic regression models in different regions of the country have already indicated that prediction accuracy for both occurrence and ecological condition differ between HGM types (Rivers-Moore and Cowden, 2012; Hiestermann and Rivers-Moore, 2015; Melly et al., 2016). However, in both case studies, these ancillary probability layers were dependent on extensive baseline wetland mapping exercises. The development of such spatial layers requires a complementary process of baseline wetland mapping and predictive model development. Baseline wetland maps provide a testing and verification dataset for model development, while the latter provides ancillary data on wetland occurrence and ecological condition to assist in improving baseline wetland inventories.

For wetland type classifications in South Africa, the Level IV classification (HGM type) by Ollis et al. (2013, 2015) is in standard use by wetland practitioners, and is in line with other global classification systems (Brinson, 1993). The classification of Level IV HGM units, including seep, depression, valley-bottom, and floodplain wetland types, also takes cognizance of inland vs. coastal systems, regional setting, and landscape position. Therefore, there is a great need for the development of refined and more robust models to allow HGM type to be identified more reliably. Here, we develop and test a simple approach for predicting the most likely HGM type for mapped yet unattributed wetland polygons.

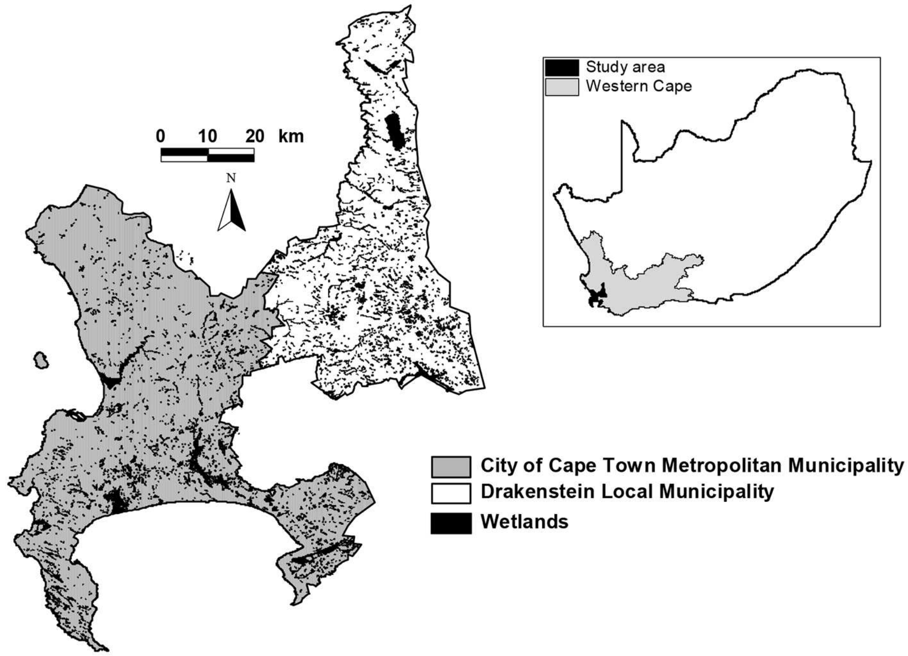

FIGURE 1 | Map of study area, showing City of Cape Town and Drakenstein municipalities and their respective wetlands datasets; inset shows context of study area within the Western Cape Province of South Africa.

METHODS

Study Area

Our study area was defined on the basis of having two reliable, adjacent and independent datasets of wetland polygons available (**Figure 1**). Both datasets describe a range of wetland types in the Western Cape province of South Africa, within the Cape Floristic region. The naturally occurring vegetation in this area is "fynbos" (a distinctive, Mediterranean climate, sclerophyllous vegetation biome only occurring on the southern tip of Africa); despite relatively high levels of land cover transformation, wetland HGM types would be generally unaffected by these changes. This is based on direct observation that climate, geology and landscape position govern occurrence and type (Hiestermann and Rivers-Moore, 2015; Ollis et al., 2015), whereas land cover transformation and degradation underpin ecological condition (Kotze et al., 2012). Underlying geology consists primarily of a mix of sandstones and fractured metasedimentary rock, interspersed with subordinate shales and mudstones; Table Mountain sandstones dominate in the west, while the Cape Fold Mountains fractured metasedimentary rocks occur in the east (Colvin et al., 2007). Topography is highly heterogeneous, with much of the study area characterized by relatively short (50–300 km) rivers in deeply incised valleys.

Datasets used for this study were the wetlands coverage for the City of Cape Town metropolitan municipality ($n = 7{,}272$ polygons; City of Cape Town, 2017), and the Drakenstein local municipality ($n = 4{,}237$ polygons; Day et al., 2009). While falling in to the same predominantly winter rainfall region, the two study areas cover a rainfall gradient from relatively wetter in the west to relatively drier in the east (mean annual precipitation gradient of ∼600–200 mm; Schulze, 1997), within a Mediterranean climate.

TABLE 1 | Node states and thresholds.

Node	State	Threshold
Elevation	Low/medium/high	Low<200<medium<500<high
Slope	Flat/steep	Flat<5<steep
Relief ratio	Low/high	Low<0.25<high
Groundwater depth	Shallow/deep	Shallow<8<deep

Within the study area, the majority of mapped wetlands have been classified to Level IV HGM type, according to the classification defined by Ollis et al. (2013). Datasets were compiled by wetland specialists, with HGM types assigned through a combination of field assessments and local terrain knowledge.

Analyses

Only inland wetlands were considered, with estuarine HGM types excluded from analyses. The number and area of HGM units per dataset were described using bar and pie charts. HGM polygons for the study area ($n = 11{,}379$) were next attributed in terms of their landscape position, shape and likely links to groundwater (Colvin et al., 2007).

- *Landscape position* included the metrics elevation (90 m digital elevation model; USGS, 2018), from which slope and aspect (both degrees) were derived using appropriate surface analysis algorithms (Clark Labs, 2009). Relief ratio, as an indication of catchment terrain roughness, was also derived from the DEM, using quaternary catchments (fourth order catchments; primary management areas for South Africa, based on a standardized mean annual runoff per unit area; Midgley et al., 1994) as the overlay image, and basin length and change in elevation (maximum minus minimum elevation) for each catchment. Lastly, HGM types were attributed by their association with Strahler stream order and geomorphological zone (upland vs. lowland, based on 1:500,000 scale river longitudinal zones with a breakpoint between upper and lower foothills; Moolman, 2006).

- *HGM polygon attributes*: Area (m^2) and perimeter (m); Log transformation of area and perimeter; shape (area: perimeter ratio—Equation 1); fractal dimension (Equation 2)

$$Shape = \frac{Perimeter^2}{Area} \tag{1}$$

$$Fractal\ dimension = \frac{2^* ln\,(Perimeter)}{\ln\,(Area)} \tag{2}$$

- Groundwater depth (m below ground; Colvin et al., 2007).

Wetland HGM data were then screened for differences in the metrics (shape, area, fractal dimension, perimeter: area ratio) between regions using a Principal Components Analysis (McCune and Mefford, 2011; correlation cross-products matrix). The purpose of this analysis was to provide an objective basis for either combining datasets or keeping them separate.

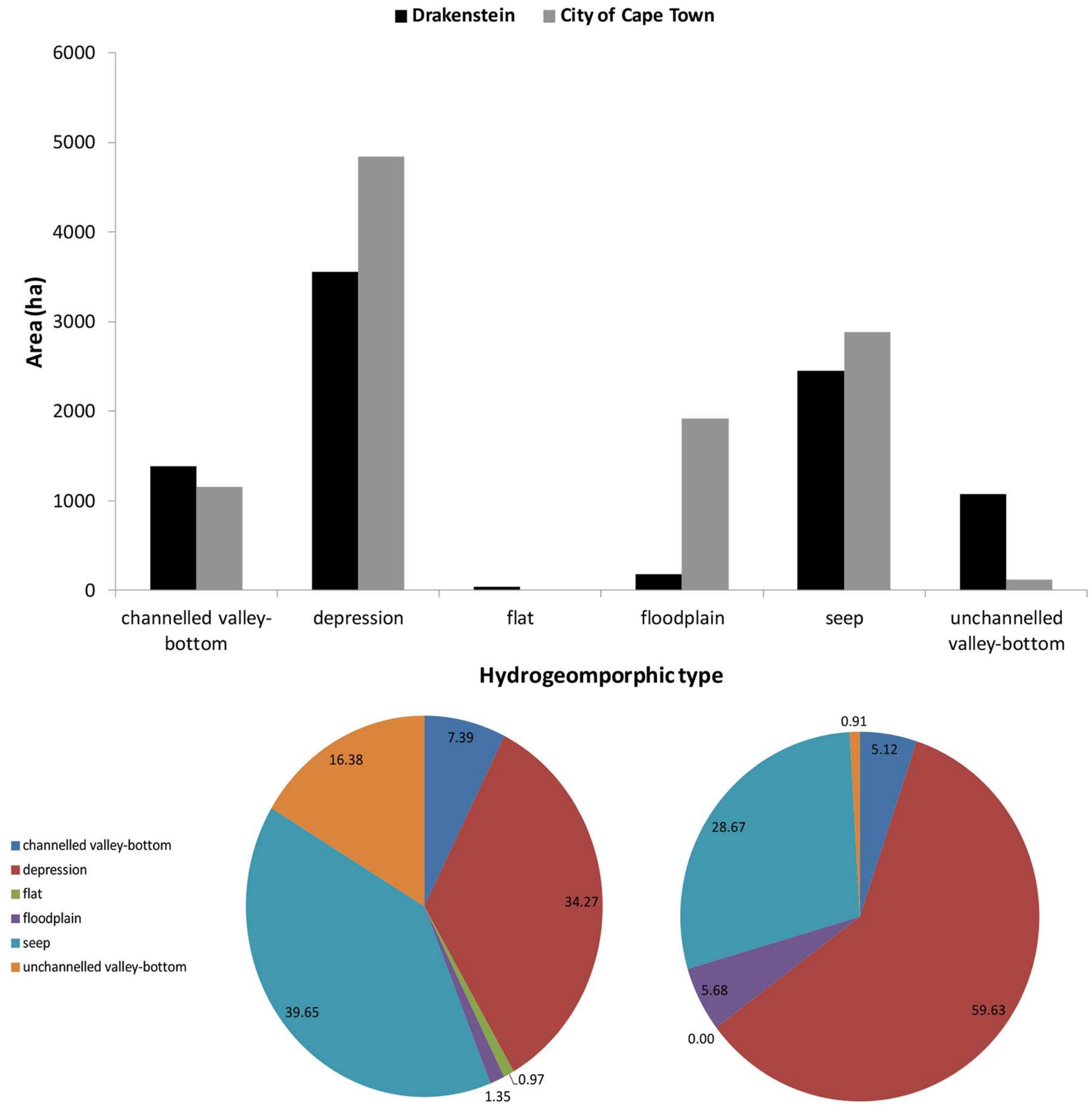

FIGURE 2 | Total area (ha) of wetlands by HGM type (top) and proportion of wetlands by HGM type for the Drakenstein (bottom left) and CoCT (bottom right) regions.

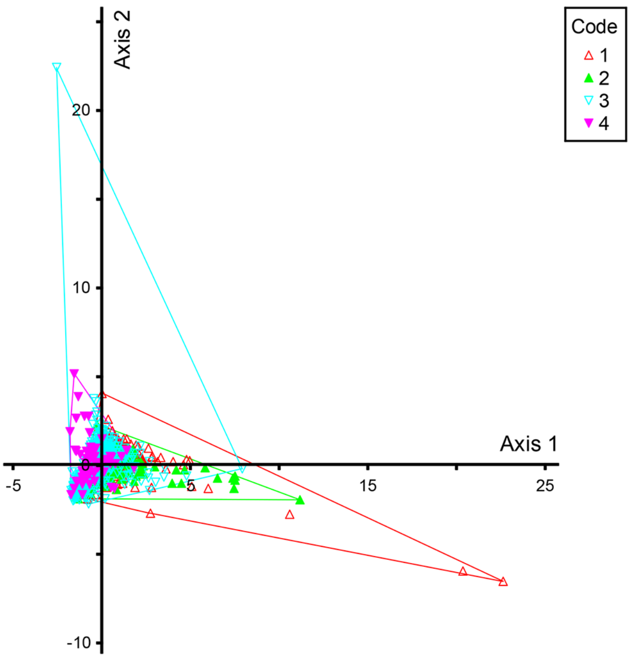

FIGURE 3 | Principal Components Analysis for channeled valley-bottom (VB-C) and unchannelled valley-bottom (VB-U) wetlands based on area, perimeter, shape, and fractal dimension. Convex hull codes: 1, VB-C (Drakenstein); 2, VB-C (CoCT); 3, VB-U (Drakenstein); 4, VB-U (CoCT).

TABLE 2 | Eigenvalues for the principal components analysis for channeled and unchannelled valley-bottom wetlands by municipality based on area, perimeter, shape, and fractal dimension.

	PC 1	**PC 2**
Cumulative percentage of variance explained	38.89	63.62
Variable		
Code	−0.216	−0.038
Area	0.604	−0.243
Perimeter	0.670	−0.071
Shape	−0.372	−0.597
Fractal	−0.047	0.761

HGM types were standardized in the CoCT and Drakenstein datasets to floodplain, seep (hillslope and valleyhead seep types merged), flat, depression (depression, isolated, and depression-linked channel types merged), channeled valley-bottom and unchannelled valley-bottom.

Next, to select variables that were useful in categorizing HGM types, we used a combination of box-and-whisker plots and a second PCA to describe HGM types by morphometric variables (R Development Core Team, 2009; McCune and Mefford, 2011). The box-and-whisker plots were used to visualize differences in median values, and data ranges, for the HGM metrics. The PCA was undertaken to assess relative importance of each metric, and which metrics were correlated to reduce metric redundancy. Thereafter, HGM types were qualitatively categorized in terms of metric traits (high, medium, and low) for eight metrics [elevation, geomorphological zone (upland vs. lowland), Strahler stream order, shape, relief ratio, groundwater depth, slope (Horton, 1932, 1945; Schumn, 1956; Gordon et al., 1992; Frimpong et al., 2005; Colvin et al., 2007)], with HGM "signatures" illustrated using a radar plot. Aspect was considered independently, by calculating the frequency of HGM types for 90° aspect arcs (north = 315–45°, etc.), plotted in a radar plot.

For the development of the Bayesian network (Bn), we excluded wetland shape because it pre-supposes the existence of a reliable wetland occurrence map. Using the optimal list of variables (slope, groundwater, elevation, relief ratio), a Bn model was developed based on four causal nodes, using Netica (Norsys Software Corp., 2010). Node states and thresholds are provided in **Table 1**. Continuous data were reassigned to node states using logical if/then statements within a spreadsheet, based on the defined thresholds. Each data record constituted a "case instance" (i.e., a unique instance of a result node based on its combination of causal nodes). Data were randomly split into training and test data (75/25% split train $n = 8{,}533$; test $n = 2{,}846$). Once the Bn had been constructed, conditional probabilities were calculated using the case file of the training data.

Model Evaluation and Verification

Model sensitivity to findings relative to the HGM node was evaluated, and verification was undertaken by testing cases against two independent case files. In the first validation exercise, we used the case test file described above i.e., the digital data. For the second validation process, we collected field information on confirmed presence and HGM type of wetlands in the study area between March and May 2019. A total of 115 wetland point locations were recorded, and classified by HGM type according to Ollis et al. (2013). These data were attributed with values for the predictor nodes; these values were then converted to node states, and a second test case file developed i.e., a field data case test file. The independent case files were used to verify the training data set used to construct the Bayesian Network. Model performance was evaluated based on four standard outputs provided by Netica: node sensitivity; frequencies of predicted vs. actual HGM types; the number of times the model was "surprised" in predictions; and receiver operating characteristic (ROC) curves for each test case file, based on sensitivity and specificity (quality of test). The ROC graph provided a visual output for assessing model performance (Fawcett, 2006).

RESULTS

In the Drakenstein study region, the dominant HGM type by area was "depression," and "seep" by number; similarly, depression wetlands dominated by area and number for the CoCT area (**Figure 2**). There was little distinction between study region for unchannelled and channeled valley-bottom types (**Figure 3**; **Table 2**) confirming that both datasets could be combined in the terms of the modeling exercise.

A PCA indicated that morphometric variables were useful in distinguishing HGM types (**Figure 4**; **Table 3**). Here, variables

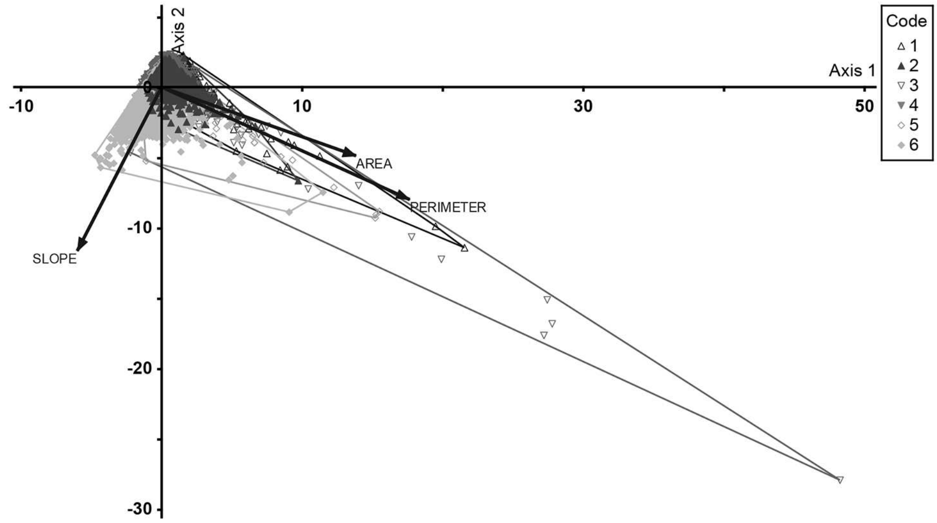

FIGURE 4 | Principal Components Analysis biplot of wetland HGM types based on polygon morphometry; 1, channeled valley-bottom; 2, unchannelled valley-bottom; 3, depression; 4, flat; 5, floodplain; 6, seep. Vectors show variables with $r^2 > 0.4$.

TABLE 3 | Eigenvalues for the principal components analysis for wetland HGM types based on morphometric values of wetland polygons.

Variable	1	2
Cumulative percentage of variance explained	16.6	32.9
HGM code	−0.3102	−0.4653
Area	0.5019	−0.3002
Perimeter	0.5677	−0.3849
Shape	−0.2714	0.353
Fractal dimension	0.002	0.0142
Aspect	−0.1308	−0.118
Elevation	0.018	−0.0082
Groundwater depth	0.0596	−0.0353
Slope	−0.3301	−0.4653
Stream order	0.3394	0.4053
Relief ratio	0.1037	0.1564

describing polygon size (shape and area) accounted for the highest amount of variation in axis 1, while landscape characteristics (slope, stream order, and relief ratio) accounted for the highest amount of variation in axis 2. While elevation and groundwater depth did not come out strongly in the PCA, the box-and-whisker plots highlighted five morphometric variables (elevation, groundwater depth, relief ratio, slope, and shape) that provided clear distinctions between HGM group types (**Figure 5**). HGM types tended to be associated with upland vs. lowland zones to varying degrees (**Figure 6**). When median HGM type characteristics for morphometric variables that offered a degree of distinguishing power were plotted on a radar diagram, each HGM signature was unique (**Figure 7**).

The relationship between these variables and HGM type were linked by conditional probabilities in a Bn (**Figure 8**). By way of examples; at high elevations, there is a 71% probability that a wetland will be a seep, and this increases to an 87.4% probability when slope is steep. Conversely, for flat areas and low elevations, the most likely HGM type is depression at 54%. In our model, HGM type was most sensitive to elevation as a predictor variable (**Table 4**), with certain HGM types (seeps and flats) being more typically associated with higher elevations, while other HGM types (valley bottom and floodplains) are associated with lower elevations. Overall, prediction accuracy for the model had an error rate of 32.5% (**Tables 5**, **6**). Notably, the HGM types with the poorest predictions were valley-bottom wetlands, which were incorrectly predicted as depressions or seeps. Conversely, prediction accuracies of seeps and depressions were high. The ROC plots further indicated that model predictions were generally good, but that the predictions were more accurate for the digital dataset than for the field-assessed HGM types (**Figure 9**).

DISCUSSION

There is a growing demand for data on the ecological condition of wetlands, which is central to tracking improvements or deteriorations in the quality of this resource (Jacobs et al., 2010; Driver et al., 2011). This requires information not only on wetland location and extent, but also type. Since ecological condition varies on the basis of landscape context and HGM type (Jacobs et al., 2010; Gutzwiller and Flather, 2011), and wetland function varies by HGM type (Weller et al., 2007), management programmes cannot prioritize wetlands for conservation and rehabilitation without knowing HGM type. Information on total area per HGM type within a region is critical for national monitoring programmes, as well as for predicting loss rates over time. While comprehensive mapping of all three components (location, type, and ecological condition)

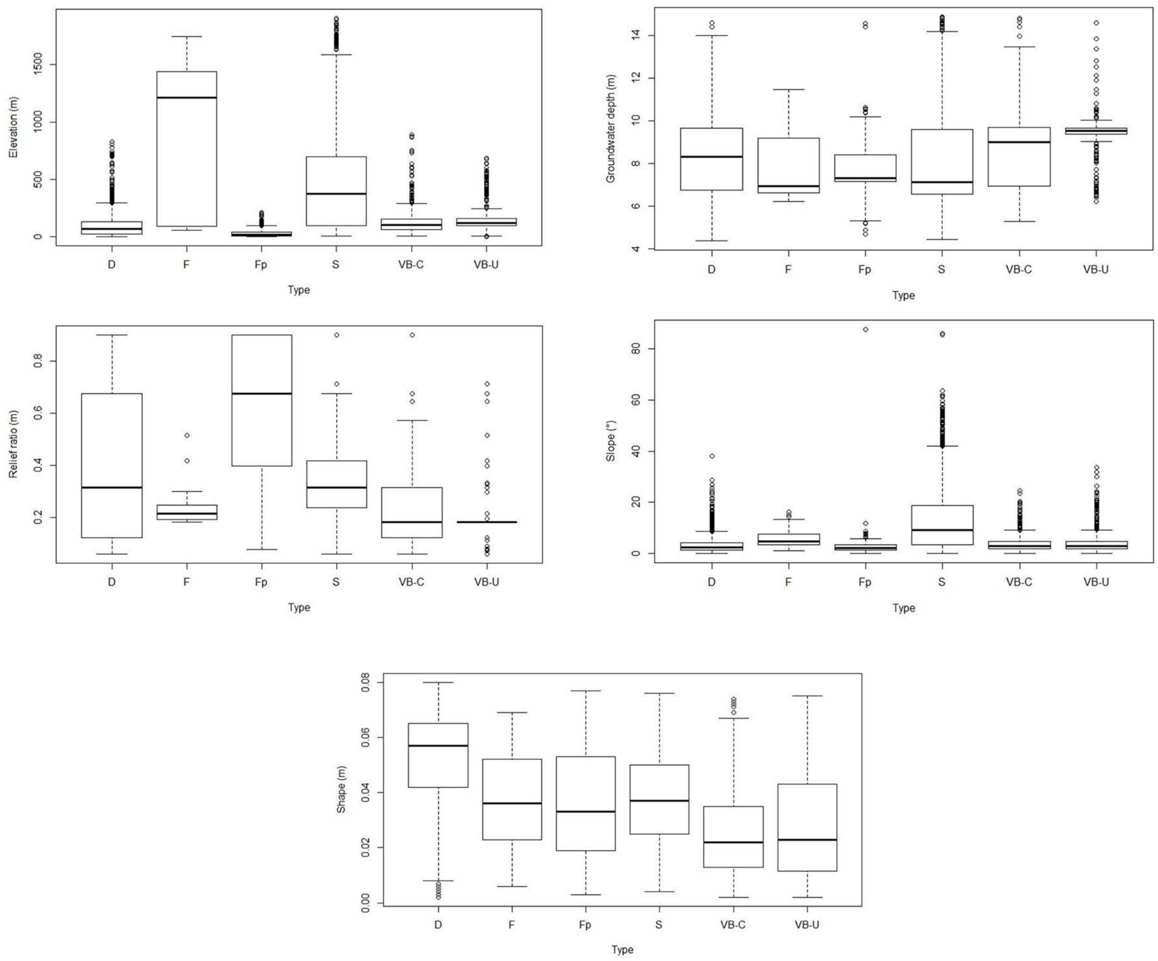

FIGURE 5 | Box-and-whisker plots of HGM type by elevation (top left); groundwater depth (m below ground) (top right); relief ratio (center left); slope (center right); and shape (bottom), where D, depression; F, flat; Fp, floodplain; S, seep; VB-C, channeled valley-bottom; and VB-U, unchanelled valley-bottom. Boxes indicate median values of metrics per HGM type plus 25th/75th percentiles, while whiskers indicate data range.

is probably the most reliable approach, probability mapping provides statistical estimates of these parameters with a high level of repeatability at a fraction of the cost (Stein et al., 2016).

Probabilistic prediction of HGM type is an innovative approach. This is because it makes use of readily available spatial coverages to predict HGM type. Excellent 90 m digital elevation models are available globally, from which slope and relief ratio can be easily derived. Global datasets of groundwater depth are also available at the same resolution (for example, Fan et al., 2013). Our approach has the advantage in that it circumvents the need to use a landform image (i.e., natural features in the landscape: valleys, hills, etc.), which has previously been a problem because of limited availability and cost of sufficiently fine-scaled digital elevation models, such as those based on light detection and ranging (LIDAR) data.

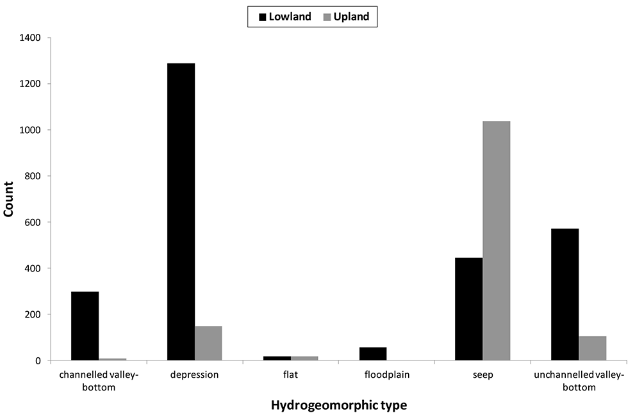

FIGURE 6 | Count of wetlands by HGM type for the Drakenstein municipality for upland vs. lowland catchments.

In general terms, our model is a useful generic approach for improving the reliability of prediction for all major HGM types with the exception of valley-bottom wetlands. The poor performance in predicting valley-bottom wetlands may be simply a result of poor learning from the case files, given the relatively low prevalence of valley-bottom types in the chosen study area. It may be the consequence of not including a size metric in the model, since valley-bottom wetlands would typically be larger than depressions. Alternatively, there are encouraging results from other studies to specifically map valley-bottom wetlands (Collins, 2017), such that a HGM typing process could be successfully achieved by using a mix of ancillary data. This would involve an initial process of identifying all valley-bottom

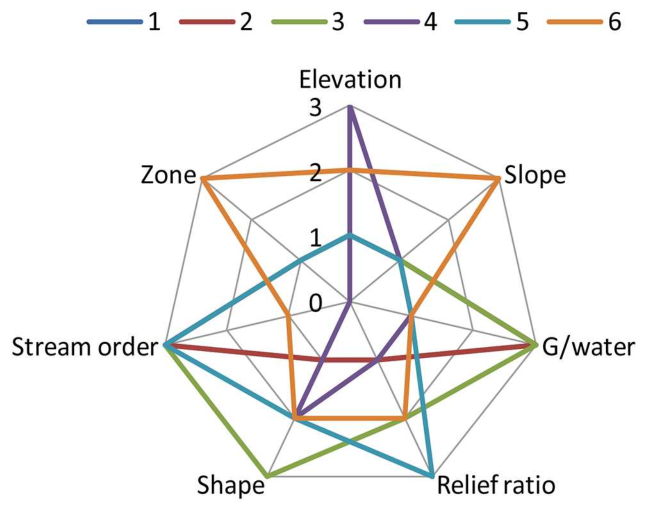

FIGURE 7 | Radar plot of HGM signatures based on qualitative median scores of morphometric variables; 1, channeled valley-bottom; 2, unchannelled valley-bottom; 3, depression; 4, flat; 5, floodplain; 6, seep. Spokes reflect variables relating to each of six HGM types, qualitatively scored according to the categories in **Table 1** in conjunction with their median values in **Figure 5**, where values 1–3 reflect categories as low/medium/high. Two additional variables (zone and stream order: Moolman, 2006) reflect HGM type majority membership for either upland or lowland zone (3, upland; 1, lowland) and Strahler stream order (1:500,000 scale).

TABLE 4 | Node sensitivity of variable nodes relative to the "HGM" node.

Node	Mutual information	Percent beliefs
HGM	1.946	100.00
Elevation	0.1244	6.38
Relief ratio	0.062	3.19
Groundwater depth	0.041	2.12
Slope	0.015	0.75

Mutual information describes the reduction in entropy in the target node (HGM) due to a finding in the variable nodes, also expressed as a relative percentage.

TABLE 5 | Predicted vs. actual assignment of wetland HGM types based on test cases.

Predicted						
Flat	**Floodplain**	**Depression**	**Seep**	**VB-C**	**VB-U**	**Actual**
0	0	3	5	0	0	Flat
0	0	113	3	0	0	Floodplain
0	0	1,260	186	0	0	Depression
0	0	258	659	0	0	Seep
0	0	114	47	0	0	VB-C
0	0	172	26	0	0	VB-U

VB-C and VB-U refer to channeled and unchannelled valley bottom wetlands.

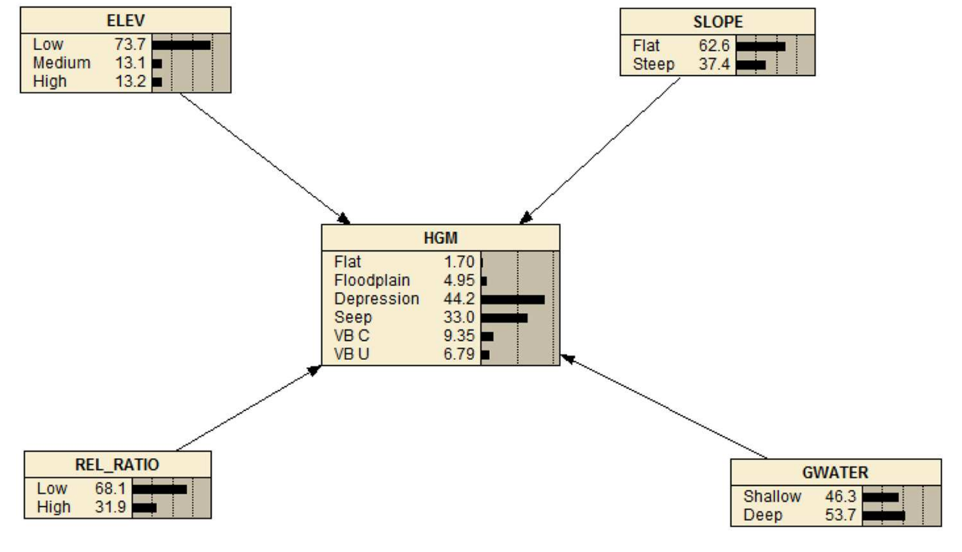

FIGURE 8 | Bayesian network model for predicting wetland HGM type based on node states for elevation, slope, groundwater depth, and catchment relief ratio.

TABLE 6 | Number of times the Bn was "surprised" for different probability values.

State	<1%		<10%		>90%		>99%	
Flat	0.12	(3/2,502)	0.28	(8/2,844)	0	(0/0)	0	(0/0)
Floodplain	0.15	(1/685)	3.44	(91/2,643)	0	(0/0)	0	(0/0)
Depression	0	(0/0)	1.49	(6/402)	0	(0/0)	0	(0/0)
Seep	0	(0/0)	0	(0/0)	4.68	(17/363)	0	(0/0)
CVB	0.88	(1/114)	4.87	(123/2,526)	0	(0/0)	0	(0/0)
UVB	0.37	(4/1,070)	1.67	(30/1,793)	0	(0/0)	0	(0/0)
Total	0.21	(9/4,371)	2.53	(258/10,208)	4.68	(17/363)	0	(0/0)

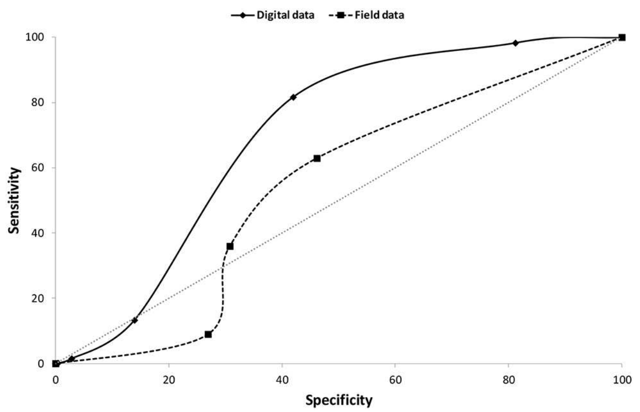

FIGURE 9 | Receiver operating characteristic curves comparing the prediction accuracy of the digital data vs. the field data for HGM type in the study area.

wetlands, followed by classifying the remaining wetlands using our model.

We recommend further research and model refinement/verification that improve the quality and resolution of input layers, and secondly in terms of translating the predictions of the Bn model to raster images of probabilities for each HGM type. For the former, consensus from the wetland scientific community on a suitable national elevation map, and an appropriate resolution (20 m: Hiestermann and Rivers-Moore, 2015; Melly et al., 2016; 30 m (USGS 1-arc minute with large voids) and 90 m (USGS 3-arc minutes void filled) will be needed. The higher the resolution of the DEM, the higher the anticipated reliability of the predictions. This would in turn form the basis for refined derived images from this map, including slope and relief ratio. For the latter, classification of the raster classes for each predictor variable into states, and subsequent translation of the HGM type model to a spatial probability product will assist with assigning HGM types to identified and mapped wetlands. This could then act as a hypothesis layer for testing against ongoing ground-truthing wetland surveys.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

Study conceived, model development, and data analyses undertaken by NR-M. DK helped with writing, structure of manuscript, and conceptual approach. NJ contributed to introduction and discussion. SM undertook field work and contributed field validation dataset.

ACKNOWLEDGMENTS

We thank the South African Water Research Commission (Project Grant K5/2546) and the South African National Biodiversity Institute for funding and support of this research.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Environmental Science

REVIEW
published: 02 June 2020
doi: 10.3389/fenvs.2020.00061

The Use of Traditional and Modern Tools for Monitoring Wetlands Biodiversity in Africa: Challenges and Opportunities

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Biodiversity is being lost in wetlands at a faster rate than any other biome. Effective conservation and management of wetlands biodiversity requires data on species status and threats to inform decision-making. However, there are key challenges in Africa around the availability, usability and quality of data, willingness to use data, and capacity. We review these challenges, using examples from Ramsar sites and other wetlands across the continent, and propose solutions to help information users access high quality data in the right format at the right time. We assess the relevance of traditional monitoring methods, as well as innovative new tools such as remote sensing and environmental DNA. We conclude by explaining how governments, civil society and the private sector can enhance data collection by applying common, policy-relevant indicators, scaling up the application of traditional and appropriate new tools and protocols, building capacity in key institutions, and using partnerships and credible science-policy interfaces. Only by sharing and upscaling the solutions to data collection and use will we be able to mainstream biodiversity into decision-making and ultimately stop biodiversity loss across African wetlands.

Keywords: capacity building, conservation, data collection, indicators, protected areas, Ramsar sites

OPEN ACCESS

Edited by:
Hong Yang,
Swiss Federal Institute of Aquatic Science and Technology, Switzerland

Reviewed by:
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National Institute of Hydrology (Roorkee), India

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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *10 September 2019*
Accepted: *29 April 2020*
Published: *02 June 2020*

Citation:
Stephenson PJ, Ntiamoa-Baidu Y and Simaika JP (2020) The Use of Traditional and Modern Tools for Monitoring Wetlands Biodiversity in Africa: Challenges and Opportunities. Front. Environ. Sci. 8:61. doi: 10.3389/fenvs.2020.00061

INTRODUCTION

The diverse wetlands of Africa, which include some of the longest rivers and some of the largest freshwater bodies in the world, are of immense importance for biodiversity and people (Thieme et al., 2005; Gardner et al., 2015; Okonkwo et al., 2015; IPBES, 2018; Ramsar Convention on Wetlands, 2018). Freshwater ecosystems cover <1% of the Earth yet they are home to more than 10% of known animals and about one-third of known vertebrate species (Balian et al., 2008; WWF, 2018). They also offer a range of ecosystem services, from water purification to hydrological buffering to coastal protection (Mitsch and Gosselink, 2000; Gardner et al., 2015). The importance of wetlands to people in Africa is further reflected by the fact the continent is second only to the Asia-Pacific region in total catch of inland fisheries (Thieme et al., 2005).

However, global wetland area may have declined by as much as 87% since 1700 (Davidson, 2014) and the downward trend for freshwater species is alarming (Vörösmarty et al., 2010). For example, in the last 35 years, the average abundance of freshwater vertebrate species populations declined by 83% (WWF, 2018), and freshwater fishes had the highest extinction rate worldwide among vertebrates in the twentieth century (Burkhead, 2012). Of the freshwater taxa in Africa that have been assessed, the most globally threatened are molluscs (41%), followed by amphibians (31%), crabs (28%), and fish (27%) (Darwall et al., 2011). These declines in aquatic ecosystems have been caused by a suite of threats, including habitat modification, fragmentation and destruction, overfishing, pollution, and climate change (Strayer and Dudgeon, 2010; WWF, 2018).

Effective conservation and management of wetlands biodiversity require data on species status and threats to inform decision-making and adaptive management. However, there are key challenges in Africa around the availability, usability and quality of biodiversity data, willingness to use data, and capacity (Stephenson et al., 2017a). As a result, many decision makers do not have access to the data they need.

We review the challenges of monitoring aquatic biodiversity in Africa, using examples from Ramsar sites and other wetlands across the continent, and propose solutions to help information users access high quality data in the right format at the right time. We assess the relevance of traditional monitoring methods, as well as innovative new tools.

THE NEED FOR BIODIVERSITY DATA FOR WETLANDS MANAGEMENT

Information on the state of the environment is necessary for informed decision-making at multiple levels across multiple sectors. For example, numerous government decisions relating to wetlands management require biodiversity data, from the development of environmental resource policies and legislation to national and landscape level planning and budgeting for resource management across sectors to the control and licensing of resource use. Biodiversity data are also required for reporting on delivery of multilateral environmental agreements (MEAs) such as the Convention on Biological Diversity (CBD), the Ramsar Convention, the Convention on Migratory Species (CMS), and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Stephenson et al., 2017a). The need for biodiversity data for assessing water-related ecosystem services and for decision-making and policy development has also been highlighted (e.g., Russi et al., 2013; Camacho-Valdez et al., 2014).

Across biomes, there is growing demand for more evidence-based conservation, with data informing decisions and evaluating performance (e.g., Segan et al., 2011; Stephenson et al., 2015a). Data needed include: species status (presence, abundance, range), offtake, trade, and threat status; habitat cover (e.g., wetlands extent) and distribution; protected area (PA) coverage and management effectiveness. For wetland sites, additional biome-specific data are often useful for management, such as water depth (Ntiamoa-Baidu et al., 1998) and the abundance and diversity of migratory waders (Ntiamoa-Baidu, 1991a), benthic invertebrates (Basset et al., 2004), and invasive mollusks (Appleton, 2003). However, the demand for data is not always being met and huge gaps remain (Revenga et al., 2005).

EXPERIENCES AND CHALLENGES OF MONITORING WETLANDS IN AFRICA

Here we present a review of the experiences and challenges identified with specific wetland monitoring around Ramsar sites and threatened species.

Ramsar Sites in Africa

Fifty African countries are contracting parties of the Ramsar Convention, leaving only four countries (Angola, Eritrea, Ethiopia, and Somalia) that are not signatories of the convention., There are 259 inland wetland sites across Africa, representing 94,777,978 ha of land area, roughly equivalent to the size of the United Republic of Tanzania, or 23 times the size of Switzerland. However, the extent of wetlands varies across Africa: in more than half of the African contracting parties to the Ramsar convention (27), Ramsar sites make up 1% or less of the total national land area. In sixteen countries, Ramsar sites cover 2–9% of the total landmass. The total area of Ramsar sites of six countries cover between 10 and 40% of the each country's total area, these being: Botswana (10%), Chad (10%), Benin (10%), Togo (11), Guinea (22%), and the Republic of the Congo (40%) (**Figure 1**).

Contracting parties (CPs) must report on the status of Ramsar sites every 3 years. However, not all CPs do so, which makes it difficult to track changes over time, on whether sites have improved or stayed the same or deteriorated. Of the 50 African contracting parties, 44 parties responded with information on status of the Ramsar sites at the COP12 (12th Meeting of the Conference of the Parties, in Uruguay, 2015). The majority of CPs reported no change (17), with slightly more reporting deterioration (14) than improvement (13). Similar to COP12, 44 of 50 African parties responded with information on status of the Ramsar sites at the COP13 (13th Meeting of the Conference of the Parties, in Dubai, 2018). Of these, 11 reported deteriorating condition, 25 reported no change, and 8 reported improving wetland conditions. Overall, between the COP12 and COP 13, most CPs reported no change (17), while 16 reported deterioration and 15 improvement. Of the sites that had deteriorated, almost half (7) deteriorated in consecutive years of reporting. Only four CPs reported sites improving in consecutive reporting periods: Cameroon, Madagascar, Rwanda, and Uganda (**Figure 1**). Overall, there appears to be a trend toward ecological deterioration of sites over time.

Ramsar Sites in Africa: Ghana as a Case Study

Ghana offers some insights into how biodiversity data are used in wetland conservation (Stephenson et al., in press). In response to a notable decline in abundance of roseate terns (*Sterna dougallii*) in the 1980s, an inventory of wetlands and water birds was conducted along the Ghanaian coast (Ntiamoa-Baidu and Hepburn, 1988). The survey covered around 50 lagoons, estuaries, marshlands, flood plains, and salt pans and was followed by monthly surveys on selected sites. The survey

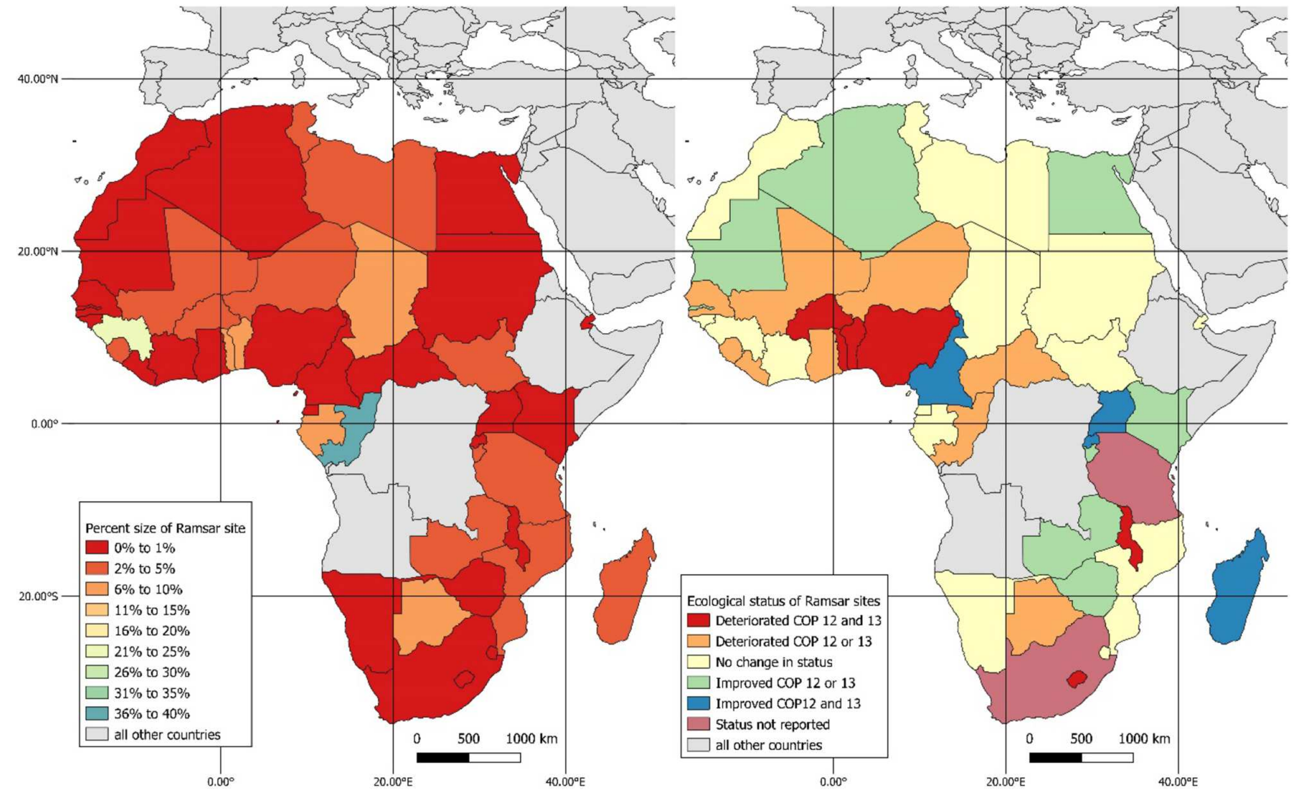

FIGURE 1 | Relative (percentage) size of inland Ramsar wetlands to country size **(Left)**. The change in ecological status of inland Ramsar wetland sites reported from COP 12 and COP13 **(Right)**. Countries where the status was not reported in both reporting periods are shown. For countries that reported in one of the two COPs, that value was included in calculating the change between reporting periods. The change between reporting periods was calculated as COP 12 plus COP 13 divided by two. Maps were produced using QGIS version 3.8 (QGIS Development Team, 2019).

data were used to identify priority sites for water birds, marine turtles and fish and a range of threats from extensive human exploitation of wetland resources (Ntiamoa-Baidu and Hepburn, 1988; Ntiamoa-Baidu, 1991b; Koranteng et al., 2000).

In turn, the bird counts provided strong justification for designating internationally important wetlands under the Ramsar Convention (Ntiamoa-Baidu and Gordon, 1991) and, in 1992, Ghana designated five coastal wetland Ramsar sites (Keta, Songor, Sakumo, Densu Delta, and Muni-Pomadze). The Ramsar designation requires monitoring of the changes in the ecological character of the site and a monitoring protocol was designed and advocated for the sites. However, the protocol required significant resourcing which was not forthcoming.

In spite of the capacity challenges, counts of water birds have continued for over three decades, initially by the local NGO, Ghana Wildlife Society, and subsequently by the Centre for African Wetlands, University of Ghana. The counts show declining populations of certain species and a reduction in the international importance of some sites. Evidence of habitat loss from encroachment by human settlement, industrial development and erosion, as well as decreases in habitat quality from pollution, has been documented through single-site studies (e.g., Osei et al., 2010; Appeaning Addo and Adeyemi, 2013). However, there are no data to feed into management interventions addressing the declining ecological status of the sites. The lack of a comprehensive long-term monitoring program, compounded by the lack of resources to manage the sites effectively and the ongoing negative impacts of climate change on coastal ecosystems, pose tangible threats to the existence of Ghana's coastal Ramsar sites.

The Ghana case is one of several examples where monitoring of birds has resulted in the creation of more protected areas and better conservation of water birds (Nagy et al., 2015). However, this study underlines trends seen elsewhere in Africa (Stephenson et al., in press), where data are often used to designate protected areas but then lack of capacity means ongoing monitoring—so vital for effective management—is lacking. While Ramsar sites are sometimes monitored through satellite-based remote-sensing to track the extent of the wetland (e.g., Dixon et al., 2016), there is a paucity of quantitative information on species and habitats and the threats they face.

Aquatic Species Diversity and Importance

An estimated 126,000 freshwater species have been described worldwide, which represents 9.5% of all described species (Balian et al., 2008). Considering that only 0.01% of the earth's surface is taken up by freshwater, aquatic ecosystems harbor a disproportionately large amount of the planet's genetic diversity.

About 60.4% of described freshwater taxa are insects, 14.5% vertebrates, 10% crustaceans, 5% arachnids, and 4% mollusks; the remaining major taxa are rotifers (1.6%), annelids (1.4%), nematodes (1.4%), and platyhelminths (1%) (Balian et al., 2008).

The above proportions show that the vast majority of described freshwater taxa (85.5%) are invertebrates. These taxa are far more diverse and phylogenetically separated than the vertebrates. Being small and numerous, they are not as well-studied, and only recently have some taxa gained recognition for their conservation importance, especially aquatic insects (dragonflies), crustaceans, and mollusks. Freshwater invertebrates live nearly everywhere there is surface or groundwater, being absent perhaps only from highly polluted surface waters and deep underground groundwaters. Densities of freshwater invertebrates can be up to $10^6/\text{m}^2$ in sediments and $10^6/\text{m}^3$ in open waters (Wetzel, 2001).

Invertebrates are functionally vital to aquatic ecosystems and can indirectly or directly affect human health and well-being. As Strayer (2006) summarizes, "invertebrates regulate rates of primary production, decomposition, water clarity, thermal stratification, and nutrient cycling in lakes, streams and rivers." Aquatic invertebrates are the primary food source for most fish species, and many vertebrate species that live in or around the water. Some species, particularly in the Mollusca and Decapoda, are harvested from the wild or farmed, supporting regionally important fisheries. Finally, some are intermediate hosts or vectors of disease, such as malaria, schistosomiasis, and river blindness, to name a few.

Dragonflies in Southern Africa

Invertebrates are rarely monitored. Standardized monitoring protocols are rare, and data are lacking on the abundance of species and changes in space and time (Cardoso et al., 2011). The situation is especially acute in freshwater systems in Africa (Stephenson et al., in press). However, some efforts are underway to monitor invertebrates and even use some insects—especially mayflies (Ephemeroptera), caddisflies (Trichoptera), stoneflies (Plecoptera), and dragonflies (Odonata)—as indicators of broader wetland health. In southern Africa, a rapid bioassessment method for rivers uses aquatic invertebrates as indicators of ecological health (Dickens and Graham, 2002). This works well, as the relative diversity of taxa is low, and there are taxonomic keys available and sufficient capacity to train technicians. The Dragonfly Biotic Index, developed in South Africa (Simaika and Samways, 2008, 2011), based on the use of adult dragonflies, has been adapted for use in rivers and wetlands throughout Africa (Vorster et al., 2020). The success of this method is largely due to the relatively low diversity of dragonflies compared with other insect taxa, their large size, their well-resolved taxonomy, public interest in these insects, and the burgeoning numbers of freshwater assessment handbooks (Samways and Simaika, 2016), field guides (Tarboton and Tarboton, 2015), and taxonomic texts (Dijkstra and Clausnitzer, 2014). The Dragonfly Biotic Index has been used to inform the ecological status of rivers (Diedericks et al., 2013), to assess the restoration of rivers (Samways et al., 2011) and succession in wetland habitats (Harabiš et al., 2013) and is therefore a model for how invertebrate data can be used for monitoring and decision-making for wetlands.

Aquatic Mammals

Small mammals are largely overlooked in biodiversity monitoring programs across Africa and Madagascar, and basic data are lacking on species abundance and distribution (Stephenson et al., in press), especially for aquatic species (Kennerley et al., 2018; Stephenson et al., 2018, 2019b). Otter shrews (a family of aquatic small mammals closely allied to the tenrecs of Madagascar) are a good example of an African taxon that is overlooked. Otter shrews inhabit waterways in the forests of Central and West Africa. They are known to feed on aquatic invertebrates, fish and amphibians yet their ecology, abundance and distribution are poorly understood (Stephenson et al., 2018).

The Nimba otter shrew (*Micropotamogale lamottei*) is endemic to a small, mountainous region of West Africa where it inhabits streams in an area $<15{,}000\ \text{km}^2$ (Stephenson et al., 2018). In spite of clearly identified threats to the species from mining (causing habitat loss and siltation) and fishing (where animals are killed in fish traps), and the importance of threat monitoring for the success of mammal conservation projects (Crees et al., 2016), there are no available data on the rate of habitat loss and the impact of hunting on this species. Its conservation status in the IUCN Red List of Threatened Species changes regularly (Stephenson et al., 2018) reflecting how scant data make it hard to assess the status of the species and plan conservation action. Therefore, further research is required to assess the distribution, abundance, habitat needs and threats of this threatened species to determine any additional conservation actions that might be needed.

Other African mammals inhabiting rivers, lagoons, and wetlands are also relatively poorly known and data deficient when compared with terrestrial mammals, examples including the African manatee *Trichechus senegalensis* (Keith Diagne, 2015), and the aquatic tenrec *Microgale mergulus* (Stephenson et al., 2019b). A training workshop organized by Wetlands International in 2010 pulled together available information on the West African manatees in Mauritania, Senegal, The Gambia, Guinea-Bissau, Guinea, and Sierra Leone and outlined threats and needed conservation action. However, information on population status is scanty and dated, and there is currently no systematic monitoring in place. The population status and trends of the African clawless otter (*Aonyx capensis*) are unknown, in spite of its continent-wide distribution (Jacques et al., 2015).

Africa and Asia are the most understudied regions for conservation research (Velasco et al., 2015). Therefore, dedicated research projects targeting key information gaps are essential. Since biodiversity monitoring in Africa is unlikely to ever focus primarily on small mammals, it may be prudent to integrate small mammal monitoring into schemes focused on larger, more charismatic species (Stephenson et al., 2019b).

Summary of Challenges

In spite of the importance of wetlands, monitoring of habitats and species is limited. If any monitoring occurs, it is usually in relation to the extent of wetlands or bird populations. These problems reflect a broader issue across Africa where challenges block access to, and use of, biodiversity data.

Barriers to using biodiversity information in decision-making in Africa include lack of availability of data, poor quality and usability of data, limited political will among key actors to collect and share data, a lack of capacity and limited resources for biodiversity research (Stephenson et al., 2017a, in press). Only 10% of recent conservation science studies were carried out in Africa, reflecting the fact that research is poorly aligned with biodiversity distribution and conservation priorities (Di Marco et al., 2017). As a result, many global data sets have taxonomic, temporal, and geographic gaps in coverage (Stephenson et al., 2015a; McRae et al., 2017). Monitoring of freshwater habitats is also hindered by resource and logistical implications and lack of data sharing (Turak et al., 2017; Hill et al., 2018). As a result, data sets on wetlands biodiversity are rarely available and often inadequate, hindering conservation planning (Van Deventer et al., 2016). Many African countries regularly census wildlife populations, yet the survey data are rarely analyzed and presented in a format that could be of direct use to decision makers (Bubb et al., 2011). In some cases, data presentation and use are influenced by a donor placing conditions on sharing.

Capacity for biological research is particularly challenging in Africa (e.g., Yevide et al., 2016; Cresswell, 2017). Integrated approaches to water and wetlands management are key, since many water issues in Africa are linked to food and energy issues (Simpson et al., 2019). However, the implementation of integrated water resource management has been difficult in parts of Africa, mostly due to a lack of experience, capacity, and resources (Claassen, 2013). Limited capacity and expertise for data sharing and use are often compounded not only by more limited resources to pay for raw images and/or data processing, but by limited internet capacity (Roy et al., 2010; Stephenson et al., in press). Many of the recent assessments of African biodiversity data have been led and conducted by scientists who are predominantly based outside the region (Beresford et al., 2013; Waeber et al., 2016). These trends reflect the fact that most of the global data sets, and most of the scientists with access and capacity to analyze them, are housed in Europe or North America. Many local communities use indigenous knowledge to make local decisions on farming and resource use (e.g., Mapfumo et al., 2016), yet this capacity is rarely tapped for more formal decision-making processes in Africa.

SOLUTIONS

In order to tackle the challenges with monitoring wetland biodiversity in Africa, we propose that governments, civil society, the private sector, and wetland scientists should enhance data collection by applying common, policy-relevant indicators, scaling up the application of traditional and appropriate new tools and protocols, building capacity in key institutions, and using partnerships and credible science-policy interfaces (**Table 1**).

TABLE 1 | Summary of responses needed to tackle the challenges with wetlands biodiversity monitoring in Africa.

Challenge	Response to challenge	Method to apply
Appropriate indicators are lacking.	Apply common, policy-relevant indicators.	Use common indicators that work at local and global scales (e.g., population indices like Living Planet Index, Dragonfly Biotic Index) when developing monitoring plans.
Indicators are not measured (inadequate collection, use, and sharing of data).	Scale up the application of traditional and appropriate new tools and protocols.	Use traditional methods such as bird counts, vegetation plots, and satellite-based remote sensing of habitats to monitor key ecosystems and species; Where appropriate to local needs and capacity, introduce, or scale up the use of, new technologies (e.g., camera traps, acoustic recording devices, drones, and environmental DNA monitoring), metrics (e.g., IUCN Green List of Species), and modeling (e.g., species distribution modeling to focus on key sites); Establish a series of pilots to test approaches for applying citizen science to wetland monitoring in Africa; disseminate lessons widely to ensure take up of successful options; Produce data products like maps and dashboards to facilitate data use and adaptive management; share data in national, regional, and global databases.
Lack of institutional capacity for monitoring and data sharing.	Build capacity in key institutions (see section Build Capacity in Key Institutions).	Governments, donors, and NGOs to make biodiversity monitoring a higher priority in conservation projects and budgets; wealthier countries to make data more accessible to high biodiversity countries; enhance the sharing of monitoring case studies.
	Use partnerships and credible science-policy interfaces (see section Use Partnerships and Credible Science-Policy Interfaces).	Academic institutions, local and international NGOs and international organizations need to support government agencies with biodiversity monitoring especially in high biodiversity countries; Scientists and decision makers from across sectors need to work together in credible science-policy interfaces that incentivize interactive dialogue and allow the joint and collaborative framing of research and policy.

In each case the response is relevant to all key stakeholders, including government departments, academic bodies, civil society organizations, and businesses.

Apply Common, Policy-Relevant Indicators

Government departments, academic institutions, civil society organizations, and businesses monitoring biodiversity should use the same core indicators across sites to facilitate the aggregation of results at national level, which enhances data sharing and allows managers to compare sites and also link results to higher-level global policy goals, such as the Aichi Targets and Sustainable

Development Goals (Stephenson et al., 2015a; Stephenson, 2019a,b).

Species abundance is still one of the most pertinent indicators for conservation (Gotelli and Colwell, 2001), and population trends should be monitored in key species. Tools available include, for example, the Living Planet Index for freshwater species (Collen et al., 2009), the wetlands extent trends index (Dixon et al., 2016), water bird counts (Sayoud et al., 2017), and the Dragonfly Biotic Index (Simaika and Samways, 2008). Sampling methods should always reflect the monitoring question being asked (Radinger et al., 2019). Wetland habitats should also be monitored with indicators such as environmental flows (King et al., 2015) and water quality (see e.g., Wronski et al., 2015). Protected area coverage and management effectiveness measurements (e.g., Knights et al., 2014; UNEP-WCMC, 2018) will provide managers with data on the level of protection offered to key wetland habitats. Threats that require research and monitoring include pollution (e.g., Olujimi et al., 2010) and invasive species (e.g., Villamagna and Murphy, 2010). In wetlands that are relied on by people for ecosystem services, other relevant indicators will be required, such as fisheries catch data (Bartley et al., 2015).

Scale Up the Application of Traditional and Appropriate New Tools and Protocols

"Observations of species and threats are most valuable when generated from systematic protocols so that data can be collected in common formats, shared, and scaled up" (Stephenson, 2019a).

Traditional Methods

Several traditional methods are working well in Africa and need to be scaled up by site managers. Where biodiversity monitoring exists at wetland sites of conservation interest it is often focused on water birds. The International Waterbird Census co-ordinated by Wetlands International (Delany, 2005) has been promoting regular surveys for many years, and bird counts offer insights into broader wetland health. Water quality measurements and benthos sampling for invertebrates have been done as single site, fixed time period studies. In terms of habitat monitoring, satellite-based remote sensing has been used to track wetlands extent and habitat over time for many years (e.g., Ozesmi and Bauer, 2002; Rebelo et al., 2018) and, although it involves technology, it can be considered a traditional technique. The tool has been used to monitor wetlands across Africa from the Niger Delta in Nigeria (Ayanlade and Proske, 2016) and Lake Bam in Burkina Faso (Moser et al., 2016) to Lake Victoria (e.g., Fuller et al., 1998) and the Akagera wetland complex (Ndayisaba et al., 2017) of East Africa. Ground truthing with vegetation plots is often useful (Ndayisaba et al., 2017; Seki et al., 2018).

Modern Methods

Satellite-based remote sensing technology is being complemented by a new generation of Earth-based sensors including camera traps (Rovero and Zimmermann, 2016), acoustic recording devices (e.g., Alvarez-Berríos et al., 2016) and unmanned aerial vehicles or drones (Wich and Koh, 2018). These sensors can enhance the quality and volume of monitoring data, reduce the fieldwork involved in data collection and, if used in systematic ways (e.g., Beaudrot et al., 2016), help fill data gaps in high biodiversity tropical countries (McRae et al., 2017). Successful uses of such devices in Africa include the use of camera traps in monitoring cryptic waterbird species (Colyn et al., 2017) and acoustic monitoring of frogs (Measey et al., 2017). Environmental DNA monitoring is another evolving technique, especially useful for tracking community composition in freshwater systems (e.g., Biggs et al., 2015; Valentini et al., 2016).

Cameras fitted to blimps (non-rigid airship systems; Hodgson, 2007) have been used to monitor river dolphins (e.g., Oliveira et al., 2017), and drones have been used to detect Sirenia (Martin et al., 2012; Hodgson et al., 2013) and monitor coastal habitats in MPAs (Castellanos-Galindo et al., 2019). However, technology alone cannot be used to monitor all species (Stephenson, 2019a), and in many cases more specialized methods are needed. For example, tests using environmental DNA to detect manatees suggests the technique "may be effective for population monitoring," especially in sites where they are in low densities or difficult to spot (Hunter et al., 2018). Valentini et al. (2016) used eDNA metabarcoding techniques to detect amphibians and bony fish and found that, "when compared with traditional surveys or historical data, eDNA metabarcoding showed a much better detection probability overall."

Other techniques that have been tested for monitoring aquatic species, including fecal DNA (Fernández-García and Cedillo, 2017) and artificial shelters (tested on desmans; González-Esteban et al., 2018), also need to be used more widely for smaller species. Techniques for lesser known species need to be integrated into standardized protocols, as has been done recently for taxa such as invertebrates and plants (e.g., van Swaay et al., 2015; Borges et al., 2018) that are often neglected.

The IUCN Green List of Species (Akçakaya et al., 2018) is a new tool to assess species recovery and conservation success that may also be relevant for many freshwater species. Early pilot testing has provided useful results for fish and amphibians, as well as aquatic mammals and birds (Stephenson et al., 2020). One advantage of the tool is that it encourages conservation planning and status monitoring across the historic indigenous range (see Stephenson et al., 2019a).

Species distribution modeling (SDM) may also be able to assist monitoring efforts by, for example predicting range shifts of species due to climate and land use change (e.g., Pauls et al., 2013) or predicting the advance of alien invasive species, and monitoring those hotspots identified in models (e.g., Bazzichetto et al., 2018). SDM has the potential to focus monitoring efforts on key sites or species, saving time and effort. WET-Health is a method developed in southern Africa for assessing the current and projected ecological condition of a wetland by measuring hydrology, geomorphology and vegetation (Kotze et al., 2018). The scope to use this tool for monitoring trends over time should be explored.

Citizen Science

Data collection requires local inputs. Equitable participation of data providers and users, including local communities, can lead to better results and sustainability (Danielsen et al., 2014). Citizen science initiatives offer an opportunity to enhance data collection and efforts should be expanded across Africa's wetlands. While citizen science schemes are most prevalent in Europe and North America, the approach is being adopted increasingly in Africa (Pocock et al., 2019). Dragonflies have been successfully monitored by school children as part of environmental education projects in Tanzania and South Africa (Clausnitzer et al., 2017). FreshWater Watch (2020) encourages people to collect data on freshwater ecosystem health and has several collection hubs in Africa. Citizen science methods developed in Europe have also been used to collect data on bird populations in Botswana, Kenya and Uganda, demonstrating that, with technical support and modest investment (c. US$ 30,000 per scheme per year), meaningful biodiversity indicators could be measured (Wotton et al., 2020). Indigenous knowledge on biodiversity can be of relevance to conservation in Africa (e.g., Sitati and Ipara, 2012; Larson et al., 2016) so more effort needs to be made to integrate local indigenous communities into citizen science schemes where appropriate.

While progress has been made with citizen science in Africa, for the approach to be scaled up, issues such as the sustainability of recruiting, training, and retaining volunteers need to be resolved (Stephenson et al., in press). In addition, data generated by citizen science need to be curated in secure, neutrally governed institutional homes—the function fulfilled in South Africa by SANBI—and converted into forms of use for decision makers, such as reports, graphs, and maps (Barnard et al., 2017).

Citizen science may be less expensive than traditional science and may offer opportunities to monitor less charismatic species, but it also requires resources to support relevant associations, online toolkits, and network portals (Chandler et al., 2017). Establishing monitoring systems, particularly in Africa, generally tend to require more investment at the outset to support training and awareness creation and to pay for equipment and materials (Bennun et al., 2005). Therefore, more pilot projects should be established by site managers to build on existing case studies to test the validity, scope, and suitable approaches for using citizen science for monitoring African wetlands. Lessons learned should be published and disseminated widely to ensure the take up of successful options.

Use and Share Data

The different individuals and organizations monitoring biodiversity need to ensure the data they collect are used for decision-making and adaptive management. Data-derived products such as maps and dashboards can simplify information and make it easier for decision makers to analyze and interpret, ultimately facilitating data use for adaptive management (Han et al., 2014; Stephenson et al., 2015a; Nel et al., 2016). "The focus should be on ensuring simplicity and on open access to underlying data and methodologies to encourage transparency and easy replication" (Stephenson et al., 2017a). Data should also be fed into relevant management systems and discussed regularly to facilitate action and lesson learning.

Data also need to be shared as widely as possible to enhance national, regional, and global data sets. Several global databases are of use to national decision makers in planning and monitoring (see https://www.speciesmonitoring.org/data--databases.html). Databases especially relevant to sharing wetlands data include:

- Aquastat (FAO; http://www.fao.org/nr/water/aquastat/data/query/index.html?lang=en)
- Global Environmental Flow Information System (International Water Management Institute; http://gef.iwmi.org/)
- International Waterbird Census Database (Wetlands International; http://wpe.wetlands.org/)
- Water Information Network System—IHP-WINS (UNESCO; http://ihp-wins.unesco.org/)
- Water Quality Index for Biodiversity (United Nation's Environment Programme's) Global Environment Monitoring System for Water (GEMS/Water; https://www.bipindicators.net/indicators/water-quality-index-for-biodiversity)
- Water-related Ecosystems (UN Environment; https://www.sdg661.app/)
- Wetland Extent Trends (WET) Index database (UNEP-WCMC; https://www.bipindicators.net/indicators/wetland-extent-trends-index).

There are also a number of biodiversity databases focused on Africa, such as FishBase for Africa (http://www.fishbaseforafrica.org/) and the ARCOS (Albertine Rift Conservation Society) Biodiversity Management Information System (http://arbmis.arcosnetwork.org/), which has data on African Great Lakes. These databases can supplement data collated by national biodiversity centers (e.g., Egypt's National Biodiversity Unit, South Africa's SANBI, Uganda's National Biodiversity Data Bank).

Build Capacity in Key Institutions

Capacity building for monitoring in relevant national institutions is essential (Stephenson et al., 2015a,b) and needs to become a higher priority in conservation projects and budgets for governments, donors, and NGOs. Bubb et al. (2011) demonstrated that, in most east and southern African countries, at least some biodiversity indicators of national relevance can be produced from existing data. In South Africa, biodiversity measures are tracked by the SANBI information system (Huntley, 2014); similar institutional structures may be useful in other African countries.

Capacity issues are often linked to resources, but "not all knowledge needs for wetland management and policy-making require cost-intensive and sophisticated monitoring" (Ramsar Convention on Wetlands, 2018). Initiating integrated biodiversity monitoring programs in sub-Saharan Africa could require as little as US$ 30–50,000 per country per year (Pereira et al., 2010; Wotton et al., 2020), and taxa for which monitoring capacity exists could be prioritized.

Wealthier countries and large conservation organizations should support African governments in realizing their data collection needs and make existing data more available. An example of such support is provided by the GlobWetland Africa Project (http://globwetland-africa.org/), a European Space

Agency led initiative with the Africa team of the Ramsar Secretariat. The project will "help African authorities to make the best use of satellite-based information on wetland extent and condition for better measuring the ecological state of wetlands and hence their capacity to support biodiversity and provide ecosystem services to human communities" (Gardner et al., 2015).

Capacity building would be further enhanced if the conservation community would learn and adapt, and "document and share examples of monitoring, with case studies of what works well and less well" (Stephenson et al., 2015b).

Use Partnerships and Credible Science-Policy Interfaces

Partnerships facilitating improved co-ordination and collaboration are key for the improvement of biodiversity monitoring (Secades et al., 2014; Stephenson et al., 2017a; Vimal, 2017). Academic institutions, local and international NGOs and international organizations have a significant role to play in supporting government agencies and it is encouraging to see that several global efforts to improve biodiversity monitoring explicitly target high biodiversity countries (Stephenson et al., 2017b; Stephenson, 2018). Some of the large biodiversity databases could be useful tools for businesses throughout project planning and implementation (see Bennun et al., 2018), so the private sector could in turn share data relevant to resource-strapped governments.

Scientists and decision makers from across sectors need to work together in credible science-policy interfaces that incentivize interactive dialogue and allow the joint and collaborative framing of research and policy (Young et al., 2014). In turn, scientists and other data collectors need to understand decision makers' priorities and information requirements and co-develop relevant tools and information products (Cowling et al., 2008). Stephenson et al. (2017a) recommend that African governments, NGOs and academic bodies test different science-policy interfaces in pilot countries or regions to see what works best, building on existing methods and support systems (e.g., Dicks et al., 2014). Existing examples of platforms, networks and partnerships to build on for African wetlands might include the AfriBES network of scientific and technical information for Africa (which focuses on south-south collaboration) and the African-Eurasian Waterbird Monitoring Partnership coordinated by Wetlands International, as well as the Ramsar-led Global Wetlands Observing System which is being piloted in Africa by the aforementioned GlobWetland Africa Project.

There may not be one common solution across Africa for improving partnerships for biodiversity monitoring. Government ministries may facilitate and build structures for dialogue around data in some countries; in others, MEA secretariats or NGOs may facilitate national-level dialogues of actors from different sectors and help mobilize resources for their functioning (such as the Nairobi Convention and its science-policy platform for regional marine environmental issues). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) could play a role, as could communities of practice, such as the NBSAP Forum (http://nbsapforum.net/) and Biodiversity Observation Networks (Wetzel et al., 2015).

CONCLUSIONS

Wetlands are vital for nature conservation and human well-being, yet our knowledge is limited on the state of biodiversity and its threats. In order to enhance monitoring, governments, civil society, academia and the private sector can enhance data collection in several ways by: (a) applying common, policy-relevant indicators; (b) scaling up the application of traditional and appropriate new tools and protocols; (c) building capacity in key institutions; and (d) using partnerships and credible science-policy interfaces.

Looking to the future, the SDGs should help stimulate an increasing number of governments to use monitoring data across sectors and encourage inter-disciplinary research and collaboration (Stephenson et al., in press). In African countries where biodiversity goals have been closely aligned with governmental development priorities, such as in Namibia (especially around communal conservancies) and in South Africa, biodiversity indicators have been used more widely and outcomes have often been positive (Tallis et al., 2008; Brown et al., 2014).

Building on successful examples of wetland biodiversity monitoring across Africa will require a concerted, collaborative effort. Governments will need to be open to collaboration with other states, with NGOs and with academia, within strong, open and transparent partnerships and credible science-policy fora. Only by sharing and upscaling the solutions to data collection and use will we be able to mainstream biodiversity into decision-making and ultimately minimize biodiversity loss across African wetlands.

AUTHOR CONTRIBUTIONS

PS and YN-B drafted the manuscript with support from JS. Spatial analyses and production of figure done by JS. All authors contributed to the final version of the manuscript.

FUNDING

IHE Delft Institute for Water Education covered the balance for the publication fee.

ACKNOWLEDGMENTS

We are grateful to our colleagues, including those in the IUCN SSC Species Monitoring Specialist Group and the Centre for African Wetlands, for ongoing discussions on how best to improve biodiversity monitoring for conservation in Africa and beyond. Comments from three helped improve the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 03 July 2020
doi: 10.3389/fenvs.2020.00095

Water Flow Behavior and Storage Potential of the Semi-Arid Ephemeral River System in the Mara Basin of Kenya

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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *24 January 2020*
Accepted: *08 June 2020*
Published: *03 July 2020*

Citation:
Wekesa SS, Stigter TY, Olang LO, Oloo F, Fouchy K and McClain ME (2020) Water Flow Behavior and Storage Potential of the Semi-Arid Ephemeral River System in the Mara Basin of Kenya. Front. Environ. Sci. 8:95. doi: 10.3389/fenvs.2020.00095

Alluvial corridors of ephemeral river systems provide viable opportunities for natural water storage in dry lands. Whilst alluvial corridors are widely recognized as water buffers, particularly for areas experiencing constant water scarcity, little research has been undertaken in Sub-Saharan Africa to explore their hydrological variability and water resource potential as alternative water sources for nearby communities. This study investigated the water flow behavior and storage potential of an ephemeral river system in the Mara Basin of Kenya for purposes of supporting water resources development and ecological sustainability. The water flow processes – including the recharge rates and water loss processes – from existing sand storage systems were established through monitoring of ground and surface water levels. Water samples along the alluvial corridor were collected and analyzed for major ions and isotopic signatures required to establish the water storage dynamics. The storage potential was estimated through Probing and Electrical Resistivity Tomography techniques, augmented with in-situ measurements of hydraulic conductivities and channel bed porosities. The mean annual storage volume in the alluvium of the study reach was estimated at 1.1 Mm^3, potentially capable of providing for the annual domestic and livestock water demands of the area. Transmission losses into the alluvium beneath the ephemeral channel-bed were noted to attenuate the flood peak discharges, depending on the level of saturation of the alluvial bed. However, water storage in the alluvium was subject to losses through evapotranspiration and seepage through fractured bedrocks. The study demonstrated the potential of alluvial corridors as water storage buffers providing alternative water sources to communities within the dry land regions with water scarcity, thereby to supporting ecosystem sustainability.

Keywords: alluvial corridors, ephemeral river systems, water storage potential, water flow processes, Mara River Basin, Kenya

INTRODUCTION

Ephemeral river systems (ERS) are a common drainage feature in arid and semi-arid regions across the globe (Hussey, 2007; Camarasa-Belmonte, 2016). Due to erratic rainfall patterns in drylands and lower buffering capacity of catchment storage, their flow pathways are a complex hydrological phenomenon (Tooth, 2000; Morin et al., 2009; Costigan et al., 2017). Normally, the flows of ERS occur for short periods, usually days or even hours, and are a direct response to heavy storm events (Berardi et al., 2013; Dogramaci et al., 2015). A distinguishing feature of ephemeral rivers in semi-arid environments is the presence of a significant volume of water storage in the channel alluvium between runoff events (Mpala et al., 2016). The volume of flow events in such systems is influenced by transmission losses to groundwater storage beneath the channel bed (Abdulrazzak and Sorman, 2006; Shanafield and Cook, 2014; Pacheco-Guerrero et al., 2017). Rapid infiltration and percolation into the unsaturated alluvium during flow events ensures continuous water availability despite the rarity of flow events (Costa et al., 2013, 2012; Jarihani et al., 2015; Rodríguez-Burgueño et al., 2017). Studies have shown that water stored within the alluvium provides an alternative source for sustainable water supply and food production during dry periods (Arnold et al., 2016; Costigan et al., 2017; Koundouri et al., 2017; Olang et al., 2019).

In ERS, alluvial corridors occur due to extreme weather conditions characterized by high variability in precipitation and temperature, leading to incomplete soil formation. The resultant soil type is usually sandy with low cohesive properties that can easily be eroded (Davies et al., 1994; Crouvi et al., 2013; Wang et al., 2014). With each flow event, sediment is mobilized and a layer of deposition builds the channel bed of the ephemeral river (Mansell and Hussey, 2005). Availability of water resources in such "sand rivers" depends largely on the frequency of flow events, the storage potential and permeability of the sands, and the importance of discharge mechanisms such as evapotranspiration, base flow and vertical leakage. Some studies have further shown that unregulated anthropogenic activities are likely to increase water demand thereby altering the hydrological and ecological regimes of such systems (Sheldon et al., 2010; Steward et al., 2012; Chiu et al., 2017).

During the last two decades, there has been an exponential increase in our understanding of ERS, which are abundant in dryland areas of Sub-Saharan Africa, the Mediterranean region as well as some parts of Australia, Chile, and the United States (Cid et al., 2017). Outstanding reviews have synthesized the existing knowledge base on ERS, highlighting their vital ecosystem services (Boulton, 2014). However, relevant to this research, previous efforts to investigate the ERS hydrological processes have emphasized only flow behavior and transmission losses (Hughes and Sami, 1992; Sharma and Murthy, 1994; Lange et al., 1997; Dunkerley and Brown, 1999; Lange, 2005; Mansell and Hussey, 2005; Mpala et al., 2016; Schoener, 2016). Some of these studies have further investigated the interaction between the transmission losses in the alluvium and its consequences on the flow behavior. Water flow behavior in alluvial corridors is largely determined by the rate of transmission losses that often reduces the discharge volumes and peaks as the leading flood wave advances downstream (Tooth, 2000; Morin et al., 2009; Costa et al., 2013). While it is today widely acknowledged that ERS alluvial corridors provide viable opportunities for nature-based water storage in arid and semi-arid regions (Hussey, 2007; Catherine and Fran, 2008; Gonzalez-carballo, 2018; Moulahoum, 2018), few studies have been undertaken within Sub-Saharan Africa to explore their hydrological variability, especially as alternative water sources for areas experiencing water scarcity. This can be largely attributed to limited information on the underlying hydrological processes, due to poor gauge networks coupled with limited infrastructure to support continuous measurements in the drylands.

Several techniques have been developed to assess hydrological variability in ERS (Shanafield and Cook, 2014). These techniques can broadly be classified into three main clusters. The first cluster entails methods – such as monitoring fluctuations in water content, controlled infiltration experiments and use of heat as a tracer – to monitor infiltration through the river bed providing point estimates of infiltration and transmission losses (Parissopoulos and Wheater, 1992; Dunkerley and Brown, 1999; Stewart-deaker et al., 2000; Dahan et al., 2008; Dunkerley, 2008; Batlle-Aguilar and Cook, 2012; Dowman et al., 2013). Although measurements of water content allow for a rapid detection of vertical infiltration rates, it is not possible to determine flux changes once stream bed sediments are saturated. Therefore, the technique cannot capture late infiltration resulting from long flood events and which may be significant in replenishing continuous natural losses from storage such as percolation and transmission flows (Dahan et al., 2008; Olang and Fürst, 2011). Hydraulic properties measured from controlled experiments are not always indicative of infiltration rates at a river-reach-scale, however, the technique provides an opportunity to estimate infiltration rates when it may not be practical to undertake sampling, particularly during flow events. A critical setback to adopting heat as a tracer to estimate infiltration into sand-beds along ephemeral rivers is that sub-surface flow is multidimensional in nature as opposed to the one-dimensional modeling provided in most thermal measurements (Amiaz et al., 2011).

The second set of techniques is based on measuring discharge during flow events to provide estimates of transmission losses over a large spatial extent (Lane et al., 1971; Pool, 2005; Harte and Kiah, 2009; Blasch et al., 2013; Rodríguez-Burgueño et al., 2017). Such methods include water balance estimates along the river reach and tracking of flood-wave fronts. Flow necessary for the water balance calculation over a reach length is typically estimated using a rating curve that provides the stage-discharge relationship. But construction of an accurate rating curve in ERS is problematic due to the flashy nature of flood waves and significant deposition and scouring that constantly alter the streambed geometry (Constantz et al., 1994; Fenton, 2018). Further, alteration of channel geometry makes it difficult to adequately parameterize over a long stretch of reaches for accurate simulation of key hydrological processes using existing models. The third group of approaches involves monitoring groundwater storage dynamics in the alluvium before, during and after flow events providing information on actual recharge into the alluvial deposits (Freyberg, 1983; Sorman and Abdulrazzak, 1993; Abdulrazzak and Sorman, 2006; Christiansen et al., 2011; Dowman et al., 2013). Application of groundwater mounding to estimate direct recharge in ERS relies on numerous assumptions, in particular, homogeneity in the porous medium and uniformity in the geological properties in the longitudinal direction (Hantush, 1967; Goodrich et al., 2013). Groundwater dating provides information on longer-term discharges and requires limited field time. However, it may not be possible to distinguish between indirect-localized recharge resulting from transmission losses and the contribution of diffuse recharge to the river-bed storage (Shanafield and Cook, 2014). Due to variations in both temporal and spatial scales of the measurement methods, processes in ephemeral rivers are at best investigated with a combination of methods. This allows constraining obvious uncertainties associated with each technique since they all have varying weaknesses and strengths.

In this study, we adopted a multi-method approach, involving quantification of the water storage potential of sand deposits in the alluvial corridor, ground and surface water level monitoring and water quality assessment for major ions and stable isotopes. We investigated the relationship between water flow dynamics, recharge into the alluvial corridors as a means of replenishing the natural water storage, and the natural processes that account for water losses in the alluvium. We further looked at the role of the sand river for water users, including groundwater dependent ecosystems.

MATERIALS AND METHODS

The conceptual approach and flow of methodologies applied in this study are presented in **Figure 1**. We conducted field measurements of event-based surface water stage and measured groundwater-level fluctuations in the alluvium using pressure transducers. In addition to in-situ water quality measurements, we collected water samples for laboratory analysis of major ions and stable isotopes. We determined sediment type and related water storage potential and permeability of the alluvium along the river reach through probing and Electrical Resistivity Tomography (ERT), augmented with in-situ measurements of hydraulic conductivities and channel bed porosities.

Description of the Study Area

The Sand River sub-catchment is located on the Kenyan side of the larger transboundary Mara River Basin of Kenya and Tanzania (**Figure 2** inset). The Sand River is an ephemeral system, occasionally flooded by high flows from highly variable rain events. The sub-catchment covers an area of 1,830 km^2, varying between 1,520 and 2,500 m above mean sea level. The terrain is gently undulating with flood plains that have rocky scarps, influenced by the present geology. Parallel ridges and intruding valleys are dominant in the study area. The lower sections of the Sand River lie within the Masai Mara National Reserve, which is globally and uniquely known for the great wildebeest migration. Rainfall distribution around the area is bimodal, with the longer season concentrated between March and June (Omonge et al., 2020). The annual potential evapotranspiration (about 500–1,200 mm) often exceeds the annual precipitation (about 300–850 mm). Annual recharge of the regional aquifer system is unknown, but climate characteristics of the basin suggest it is small. The daily mean temperatures vary between 17 and 22°C.

The main geology is the rock basement system composed of three main metamorphic rocks; gneiss, quartzite and schist (**Figure 2**). These rocks underlay a superficial layer that forms part of the upper unconfined shallow aquifer. Dominant soil types are clay, clay loam, sandy-clay-loam and sandy-loam (Defersha et al., 2012; Mwangi et al., 2016). Sandy soils are reddish brown surrounding muscovite-quartzite and quartzite rock outcrops in the hilly areas of the sub-basin. Dominant natural vegetation covers in the sub-basin are grasslands and savannah, covering 50 and 28% of the land area, respectively. Fragments of natural and planted forests cover 10% of the total sub-basin area and are concentrated on hillslopes. Shrubs cover 12% of the sub-basin. Economic activities include livestock husbandry, small scale irrigated farming and tourism with livestock keeping being the main source of livelihood in the area (Lamprey and Reid, 2004). Tourism is related to the nearby national reverse and provides an alternative source of income. Socio-economic development is highly dependent on the available water resources in the ephemeral river system.

Estimate of Water Storage Capacity of the Alluvial Corridor

We produced a two-dimensional (2-D) model of the sub-surface resistivity using an ABEM-1000 Terrameter with 41 electrodes attached to a multi-electrode cable spanning 200 m for 8 profiles and 120 m for 2 profiles at selected sites along the reach length as indicated in **Figure 2**. The ground resistivity obtained from these electrical resistivity tomography (ERT) surveys was related to parameters such as sediment/rock type, porosity and water content (Loke, 2000; Pánek et al., 2008). The Wenner configuration, which has a high sensitivity to vertical changes in resistivity and the strongest signal strength due to its low geometric factor was chosen for electrode configuration. A 5 m electrode spacing was adopted for the first 8 profiles and changed to 3 m for the last 2 profiles to better capture the depth of alluvial deposits at two sites. Measurements were stored in the instrument and downloaded later using ABEM Terrameter SAS4000/SAS1000 Software for inversion in the RES2DINV software (Araffa, 2009). We confirmed the depth of the sand deposits by driving a metallic rod into the sand layers; an approach commonly referred to as probing. Four sites in the upstream of the Sand River sub-catchment were chosen for probing. We noted the depth to the bedrock including elevations and coordinates of the probing points. Probing intervals of 10 and 3 m were adopted for longitudinal and transverse sections respectively. Porosity was measured on site by filling a container of known volume with sand from the probed sections, and adding water to saturation. An approximate value of effective porosity was assumed to be the ratio of the volume of water that saturated the sand to the volume of the container (Mansell and

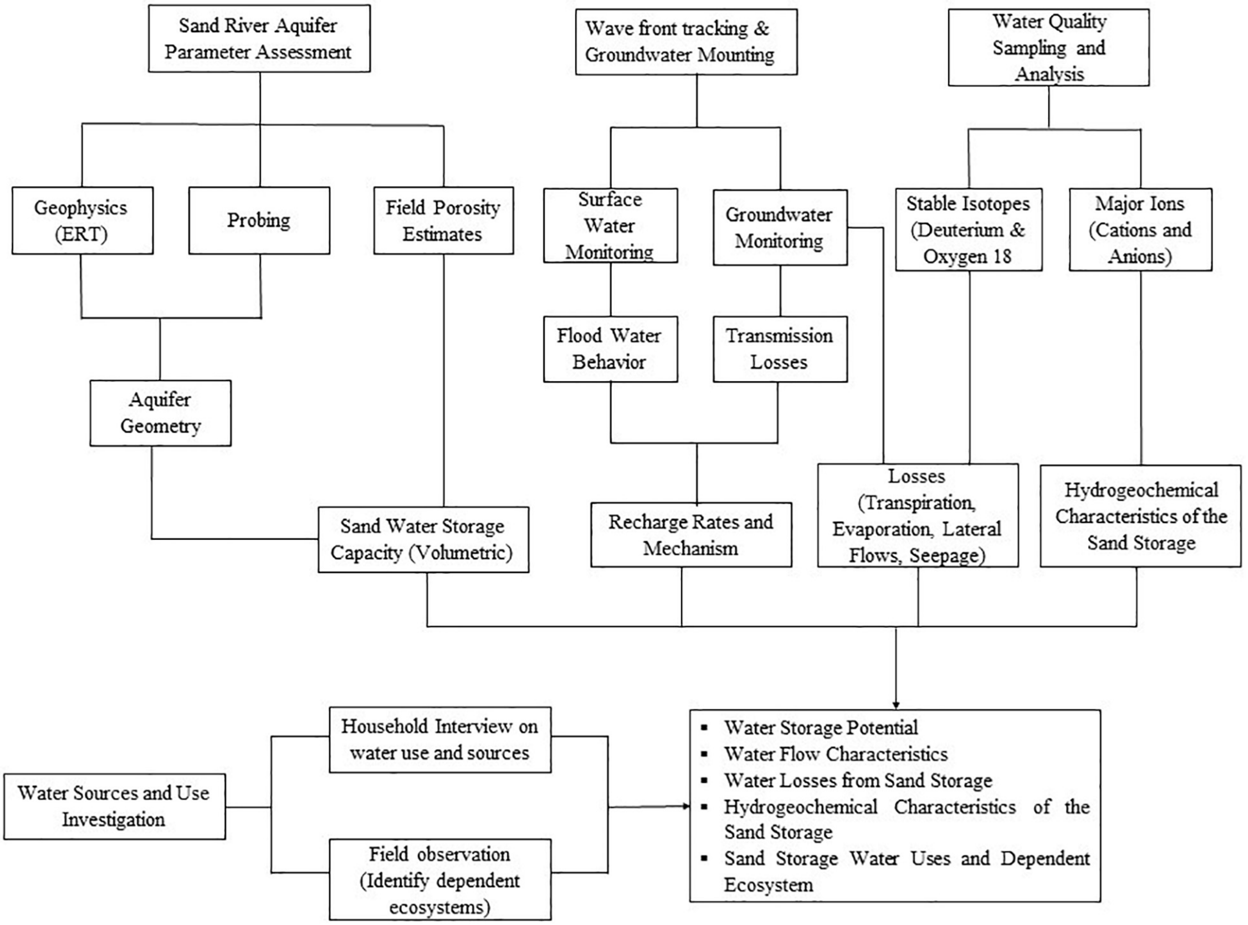

FIGURE 1 | Conceptual approach of the study: flow of methodologies. A three-step multi-method approach was adopted: (1) Desktop study and data collection planning; (2) Field investigations; and (3) Data processing and analysis. Applied techniques cut across the three main group of techniques available to study ephemeral rivers (Shanafield and Cook, 2014).

Hussey, 2005). In this case, the sand was disturbed and thus we attempted to achieve some degree of the natural state by gently compacting before saturating with water. Due to limited data available, potential evapotranspiration, which was considered as a sink to sand storage, was estimated based on the Blaney and Criddle approach (Rahimikhoob and Hosseinzadeh, 2014; Hafeez and Khan, 2018). The resultant potential evapotranspiration was then used to estimate the reference evaporation that is often taken as open water evaporation (Han, 2018; Xiang et al., 2020).

Groundwater and Surface Water Monitoring

We made groundwater and surface water measurements at selected sites in upstream sections of the Sand River in the vicinity of the ERT measurements (**Figure 2**). A piezometer was installed in the middle of the streambed to measure groundwater level fluctuations in the shallow alluvial aquifer (**Figures 3A–C**). Measurements for groundwater levels were taken at 15-min intervals using a submersible Mini-Diver pressure transducer installed at a depth of 1 m below the surface and with a pressure range of 1,000 cm H_2O (Kaasinen, 2003; Freeman et al., 2004). Similar pressure transducers were used to monitor the surface water stage, approximately 10 m upstream of the installed piezometer (**Figures 3A,B**) and water level fluctuations in a water pool opposite the location of the piezometer (**Figures 3A,C**) with measurements made at 15-min intervals as well. To obtain the exact depth of water above the divers, raw readings from the transducers were corrected by barometric compensation using measurements of air pressure from a Baro-Diver (Schlumberger Water Services, 2007).

Water Sampling and Analysis

We collected water samples along the entire Sand River stretch from both groundwater and surface water (pools, sand and flowing surface water). Two samples were collected per site for major ions. 50 ml sample bottles for both anions and cations were filled with water filtered through 0.45 μm pore size filters. For cations the samples were acidified with 2–3 drops of 65% Nitric acid (Appelo and Postma, 2006) to prevent oxidation, stop bacterial growth and minimize precipitation

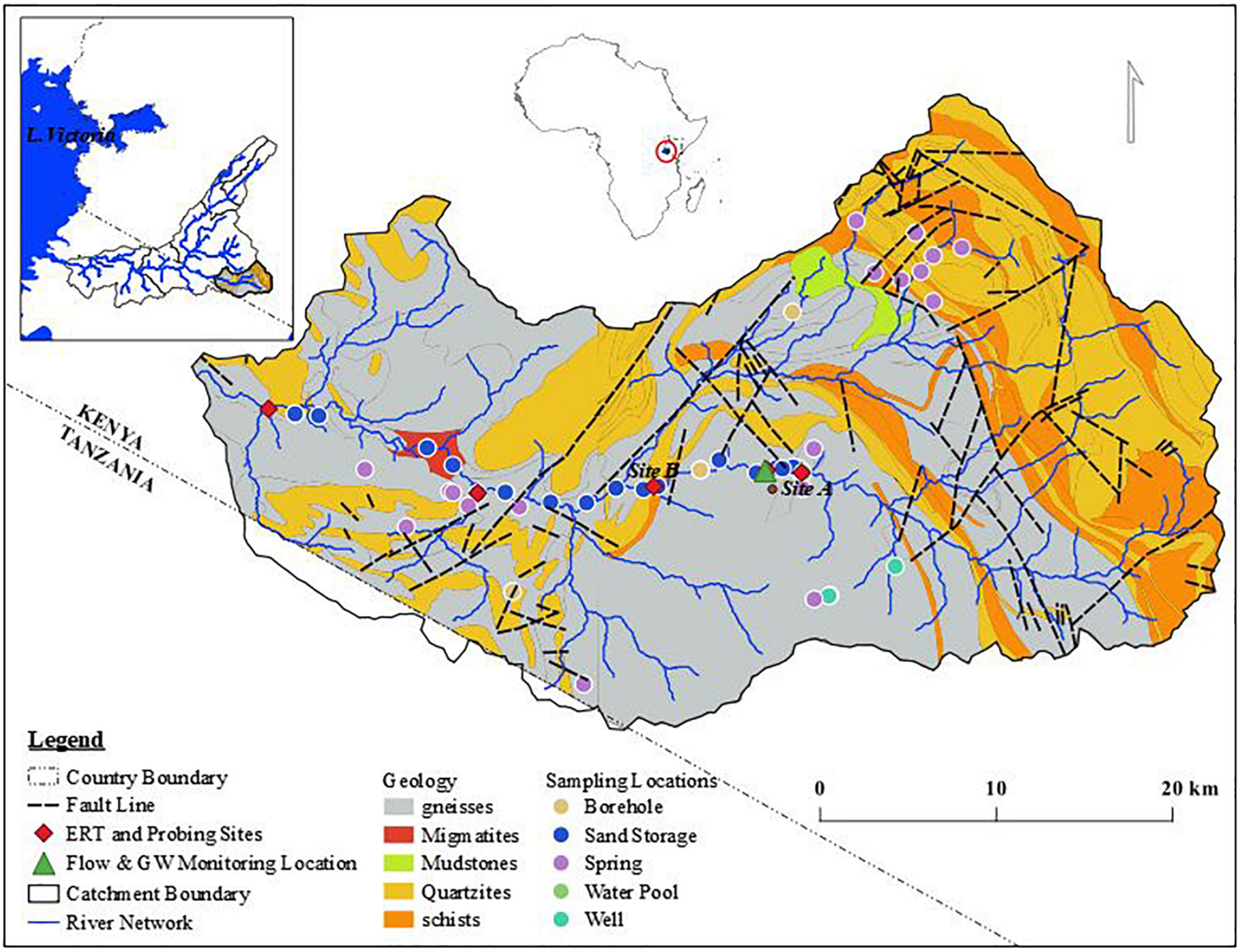

FIGURE 2 | The Sand River sub-catchment, indicating the hydro-geological properties, local surface geology, study water points, and sampling and survey locations.

or adsorption of cations that would otherwise change the chemical composition of the sample. All the samples were then stored cool at 4°C. Samples for stable isotopes (Oxygen-18 and Deuterium) were neither filtered nor stored in regulated conditions. Care was only taken to prevent evaporation of the sample during storage and transportation with double-capped 1 ml glass bottles. Temperature, electrical conductivity (EC), pH, Alkalinity and chloride (Cl) were determined in-situ. Alkalinity is prone to changes and therefore has to be measured in-situ. Conductivity, pH and temperature were measured with probes. A field titration Hach Kit (Hutton, 1983; Bartram and Pedley, 1996) was used to measure alkalinity and Cl with 0.2 M sulphuric acid/bromocresolgreen-methylred indicator for alkalinity and silver nitrate/potassium as reagents for alkalinity and Cl, respectively. Major ions (sodium, magnesium, calcium, nitrate chloride and sulfate) and stable isotopes (Oxygen-18 and Deuterium) were analyzed in the laboratories of IHE Delft, The Netherlands. Spectrometry (Rosenberg and Panne, 2014) was used to measure major cations in which atomic absorption was adopted for magnesium and calcium and atomic emission for sodium. Ion chromatography was used to measure major anions. An LGR liquid water isotope analyser was used to measure stable isotope concentrations and results are reported relative to Vienna Standard Mean Ocean Water (Mook and Geyh, 2000).

Water Sources and Use Investigation

We conducted household interviews to establish the existing water sources supporting varying demand sectors across the catchment. Two main strata were considered representing the two administrative boundaries that form part of the catchment. The stratified sampling technique was adopted for the strata classification since it minimizes errors by ensuring that all the dimensions of a particular target population are included and therefore increases survey efficiency. We further sub-divided the two key strata into multiple sub-strata based on the perceived existing water demand sectors. Main water sources initially envisaged to exist in the study area prior to the household survey included the storage in the alluvium along the Sand River, (un)protected springs, wells and boreholes. Location of the persons interviewed, including water sources, were mapped using the Garmin GPSMAP 64 geographical positioning system. Statistical analysis of the data captured

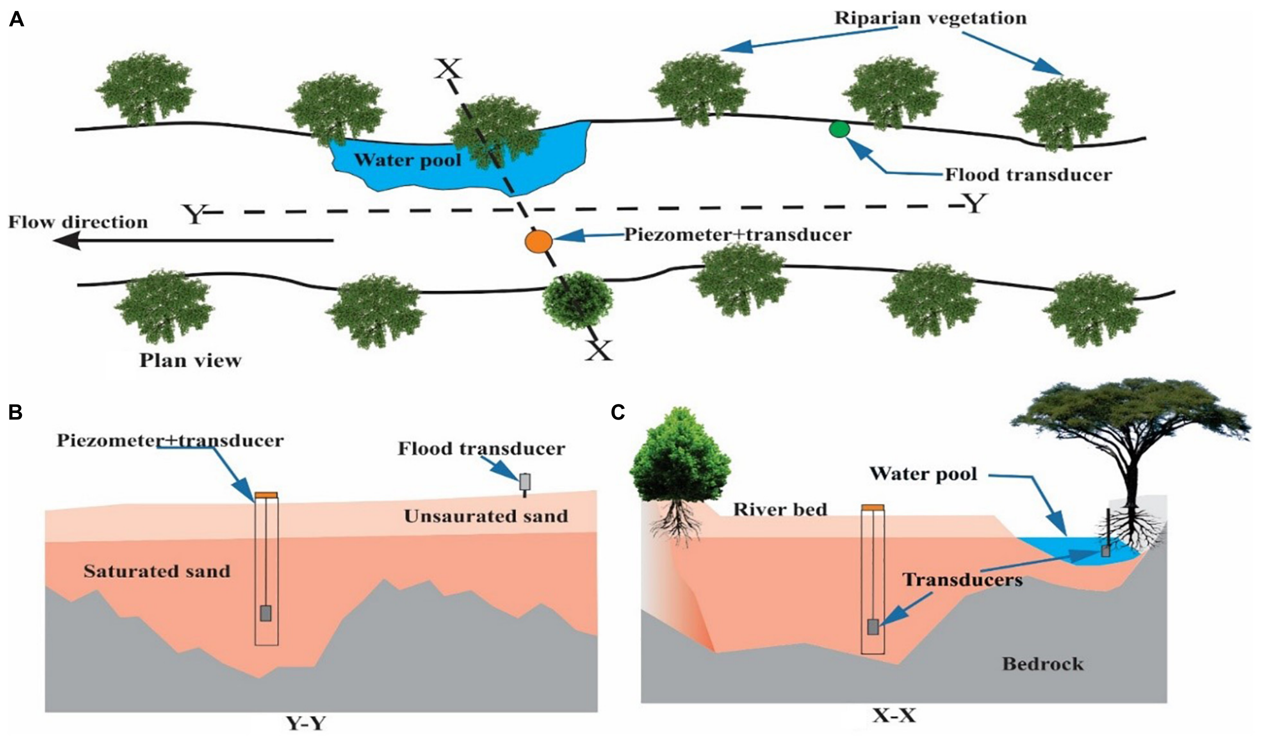

FIGURE 3 | Schematic representation of groundwater, surface flow, and water pools monitoring transducer installations in the upstream of the Sand River sub-catchment between November and December, 2016. **(A)** Plan view, **(B)** Longitudinal (Y-Y) section and **(C)** Transverse (X-X).

was done using the Microsoft Excel spreadsheet and the resultant excel database converted to GIS database using QGIS software.

RESULTS

Storage Potential

Alluvial Corridor Geometry

Aquifer geometry and sand properties determine the storage potential in the sand deposits along ephemeral river systems. Subsurface resistivity along the river ranged from 10 to 1,280 Ωm (**Figures 4A,B**). Very low resistivity between 10 and 15 Ωm on either side of the riverbanks (bottom graphs of 4A/B) revealed clay-rich sediments in the subsurface, whereas the highest resistivities (above 400–500 Ωm) reveal the occurrence of (partially fractured) bedrock. The probing results illustrate the undulating nature of the bedrock, creating natural micro reservoirs that impede downstream flows within the sand deposits. They further reveal the limited thickness of the sand river deposits and shallow depth of the bedrock, ranging from 0 m (at rock outcrops) to a maximum of 2 m (**Figures 4C,D**). Both the longitudinal and transverse resistivity profiles at site A illustrate the presence of water at greater depths (as shown by intermediate resistivities, 20–160 Ωm) and thus a possible existing connectivity between the sand river alluvial aquifer and the regional aquifer system. The occurrence of downward or upward flow depends on the differences in hydraulic head between the two aquifers. However, ERT profiles could not distinctively show the depth of the shallow alluvium even at 3-m electrode spacing.

Water Sand Storage Potential

The potential of water storage in the alluvium along the sand river was estimated for sections A and B, which are 10 km apart (**Figure 2**). Based on the estimated aquifer geometry determined by probing depth and measuring width along the reach length, the potentials of water storage at full capacity for sections A and B are 6,810 and 2,757 m^3, respectively. The sand medium was assumed to be isotropic with a uniform field measured total porosity of 33%. The volume estimates were based on lengths of 400 and 210 m for the two sections (**Figures 4C,D**). Considering the length of the two sections, storage potential per unit length (m) is 17 and 13 m^3/m for sections A and B, respectively.

Water Flow Characteristics

Surface Flow Behavior

Historical stage measurements from the downstream of the Sand River record high flow variability (**Figure 5A**). Observed water levels <0.3 m were considered as a non-flowing or dry river. At a gauge height of 0.7 m, there was a major deflection point on the frequency exceedance curve. We adopted this level as a flood event threshold. Frequency duration analysis indicated that 37 dry spells occurred between July 2013 and January 2016. 30% of the dry spells lasted for a

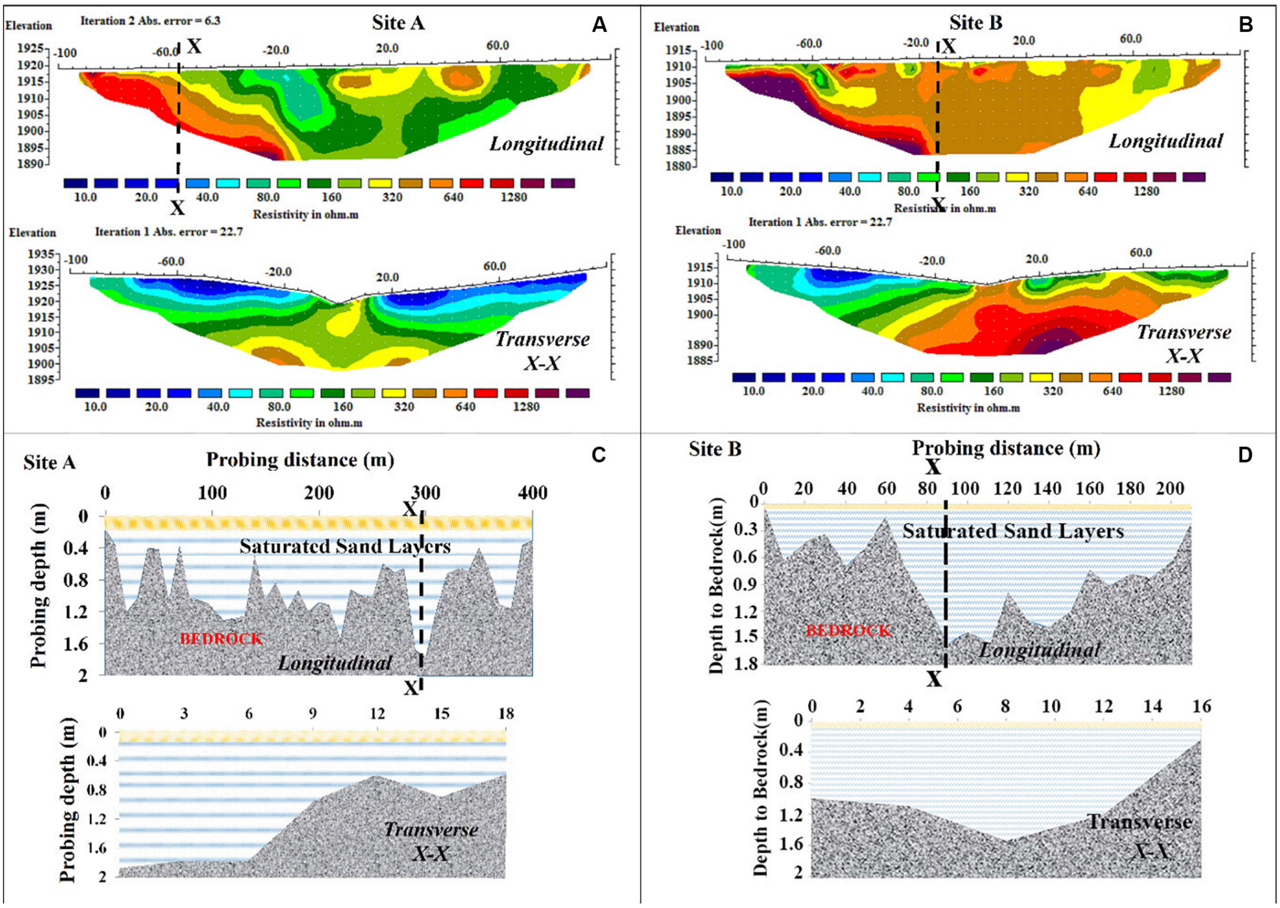

FIGURE 4 | Longitudinal and transverse profiles of resistivity **(A,B)** and probed bedrock depths **(C,D)** undertaken at sample sites A and B.

maximum of 2 weeks while the rest persisted for more than a month. The longest dry spell and flood event in the 31-month period lasted for approximately 4 months and 2 weeks, respectively. Our flow stage measurements performed in the field between the 23rd and 27th of November 2017 at a selected site in the upstream of the catchment captured two significant flood flow events (**Figure 5B**): one of maximum 33.3 cm that occurred on the 24th and one of maximum 89.9 cm that occurred on the 25th. A smaller event was also captured on the 27th.

Transmission Losses and Recharge

Measured hydrographs for the floodwater and groundwater recharge in the alluvial corridors exhibit similar characteristics; steep rising and gentler recession limbs with a lag in time of rise (**Figure 5C**). The recession limbs were clearly noted to have a longer duration. A recharge process observed on the 24th of November after a rain event indicated a steady rise in groundwater level to full aquifer saturation in 1.5 h. The sand deposits remained fully saturated with minor fluctuations until the floodwater peaked, after which both hydrographs, groundwater and surface water, receded at a similar rate. The groundwater level in the alluvial deposits remained at a higher level than before the flood onset and subsequent infiltration, percolation and recharge. The rising limb of the groundwater hydrograph defines the rate of recharge while the difference between initial and final groundwater levels defines the amount of transmission losses. A recharge rate of 0.6 cm/min resulted in a recharge magnitude of 0.34 m. Assuming isotropy in the aquifer with porosity and uniform river width of 33% and 15 m, respectively, estimated recharge volume occurring per unit length is approximately 1.7 m^3.

Losses From the Sand Storage

Losses from the aquifer due to direct evaporation are evident by the stable isotope composition in the water samples collected along the Sand River (**Figure 6A**). Isotopic ratios ranged from 7.1 to -19‰ and 0.89 to -3.8‰ for Deuterium (δ^2H or δD) and Oxygen-18 ($\delta^{18}O$), respectively. The gradient of a straight line fitted to the data points is 5.64, a value less than 8.13 and 7.68, slopes for the Global Meteoric Water Line (GMWL) and Local Meteoric Water Line (LMWL), respectively. Zooming into the sub-daily data for the water pool inside the sand river (**Figure 6B**) reveals that the water level in the pool and sand deposits drops during the daytime and stabilizes

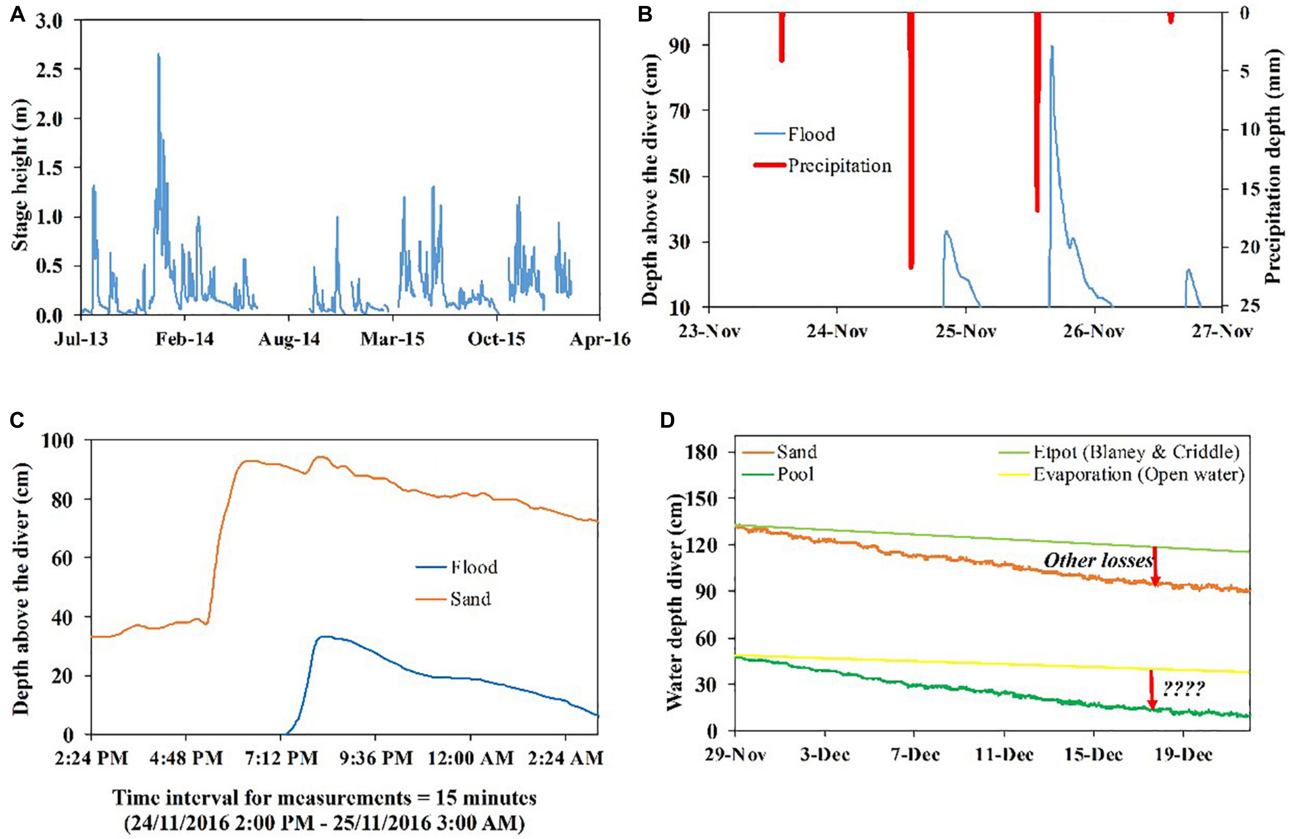

FIGURE 5 | (A) Hydrograph at sand river gate gauge site; **(B)** flow responses based on individual rain events; **(C)** recharge and flood dynamics; and **(D)** losses in the sand storage due to evaporation and transpiration, as well as other losses to vertical and lateral flow. Surface water and Groundwater monitoring were undertaken at the site indicated in **Figure 2**. However, historical measurements were for the existing gage station further downstream.

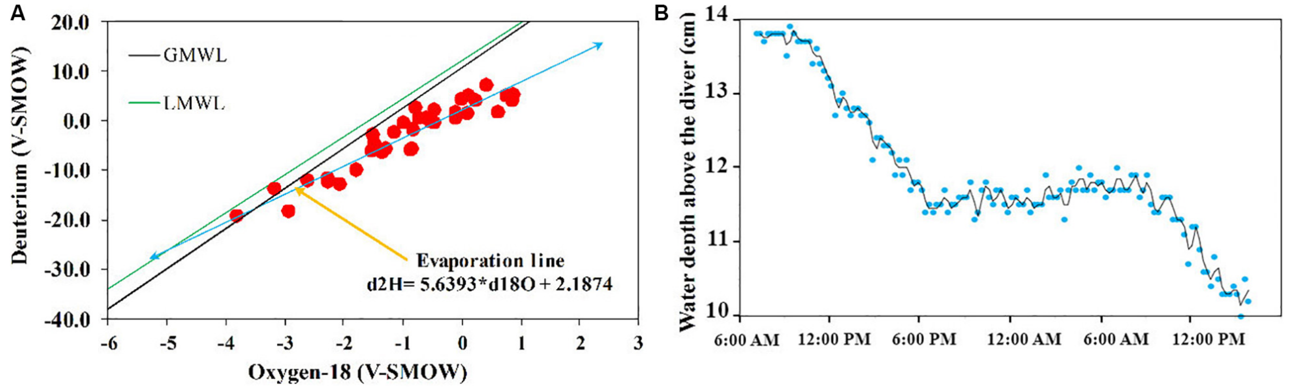

FIGURE 6 | (A) Isotopic composition for samples from the sand deposits; **(B)** Diurnal fluctuations in water level obtained from water level measurements in the pool.

during the night (**Figure 6B**). The drop of 30 mm is too high for evaporation alone; uptake and transpiration by riparian vegetation must play an additional role. No drop in water level occurs at midnight. Maximum increase in water level rise ensues between midnight and 4AM, an indication of lateral inflow from the aquifer. **Figure 5D** illustrates that losses in the Sand River are higher than only from evapo(transpiration), as the drop in water level over time needs to be explained by other losses.

Hydro-Geochemical Characteristics of the Sand Storage

Groundwater in the alluvial storage is mainly characterized by a Ca-HCO_3 water type (**Figure 7**). Calcium and sodium are the

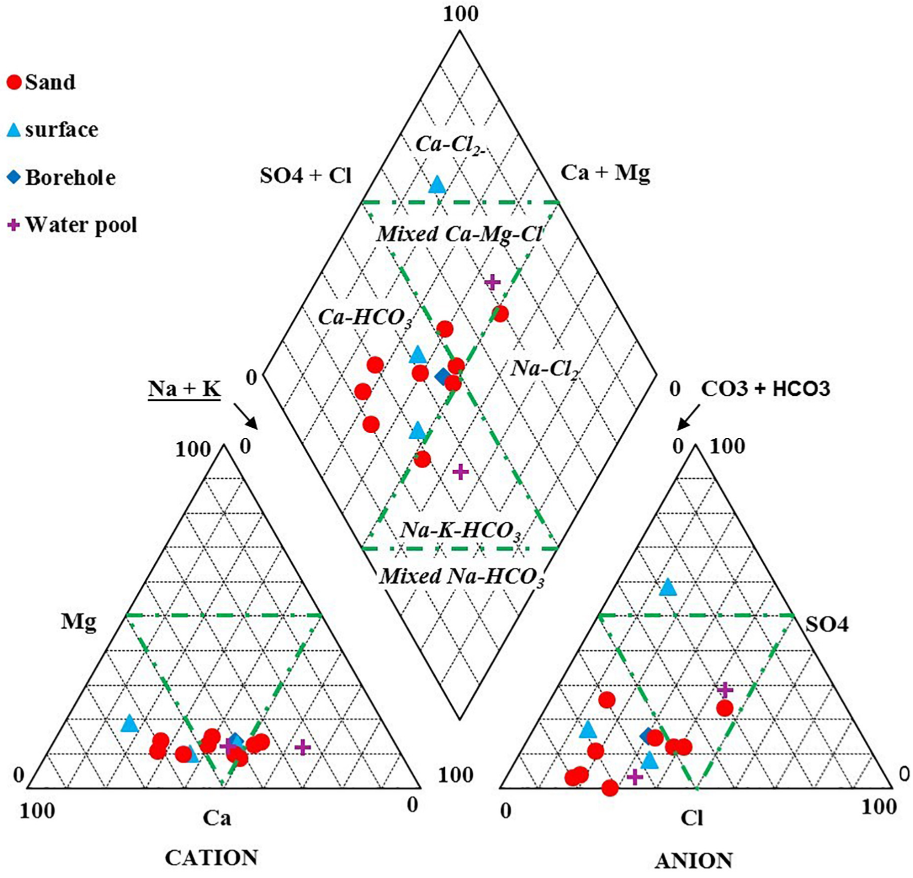

FIGURE 7 | Surface water and groundwater samples collected from the Sand River (Alluvium, surface flow, storage in the water pools) and boreholes plotted in a Piper-Trilinear diagram.

main cations while bicarbonate is the main anion. The presence of Na^+ and Ca^{2+} is attributed to the geological formations of the study area, in particular gneiss and schist, which are composed of silicate minerals rich in Na^+ and Ca^{2+}. Upon weathering the incongruent dissolution releases these cations and produces HCO_3^- through reaction with dissolved CO_2. This causes the Na/Cl ratio in the water samples to exceed the seawater ration of 0.86 (**Figure 8F**). Surface water in the discrete isolated water bodies along the Sand River presents two distinct water types: $Ca\text{-}HCO_3$ and $Ca\text{-}Cl/Ca\text{-}SO_4$ suggesting different environments drive the chemistry. Surface water chemistry indicating $Ca\text{-}HCO_3$ water type is revealing the signature of the alluvial aquifer, indicating groundwater stored in the alluvium is discharged to the surface at some point. The $CaSO_4/CaCl$ water type represents run-off, with a low bicarbonate concentration and somewhat higher sulfate and chloride concentrations due to evaporation.

Calcite saturation in the collected samples is directly proportional to alkalinity (**Figure 8A**). All the waters from the sand deposits are in equilibrium or slightly super-saturated with calcite. Supersaturation seems enhanced by evaporation as revealed by higher Cl concentrations (**Figure 8B**) and a positive correlation with calcite saturation in some samples. In more evaporated groundwater samples, calcite precipitation has already occurred, lowering the saturation index again. CO_2 pressures in the sand deposits range from $10^{-1.5}$ atm, typical for groundwater passing through soils richer in CO_2, to $10^{-3.0}$ atm, almost in equilibrium with the atmosphere (Appelo and Postma, 2006) (**Figures 8C,D**). CO_2 pressures of the water pools confirm their hydraulic connection to the alluvial aquifer (**Figure 3C**), and the same holds for the river water, although lower CO_2 pressures do reveal degassing taking place (confirmed by a high calcite supersaturation in one of the samples). Fluoride concentration in water along the Sand River is almost everywhere above 1.5 mg/L (**Figure 8E**), the admissible maximum concentration based on WHO guidelines. The relationship between sodium and chloride gives even more insights into the hydrogeological processes that occur in the alluvial aquifer altering the chemistry of the recharged water (**Figure 8B**).

Sand Storage Water Uses and Dependent Ecosystems

Water storage in the alluvium supports local livelihoods and diverse ecosystems. Local people informed us they use water in the alluvium to support their own domestic needs as well as their livestock needs. Abstractions for livestock and domestic water

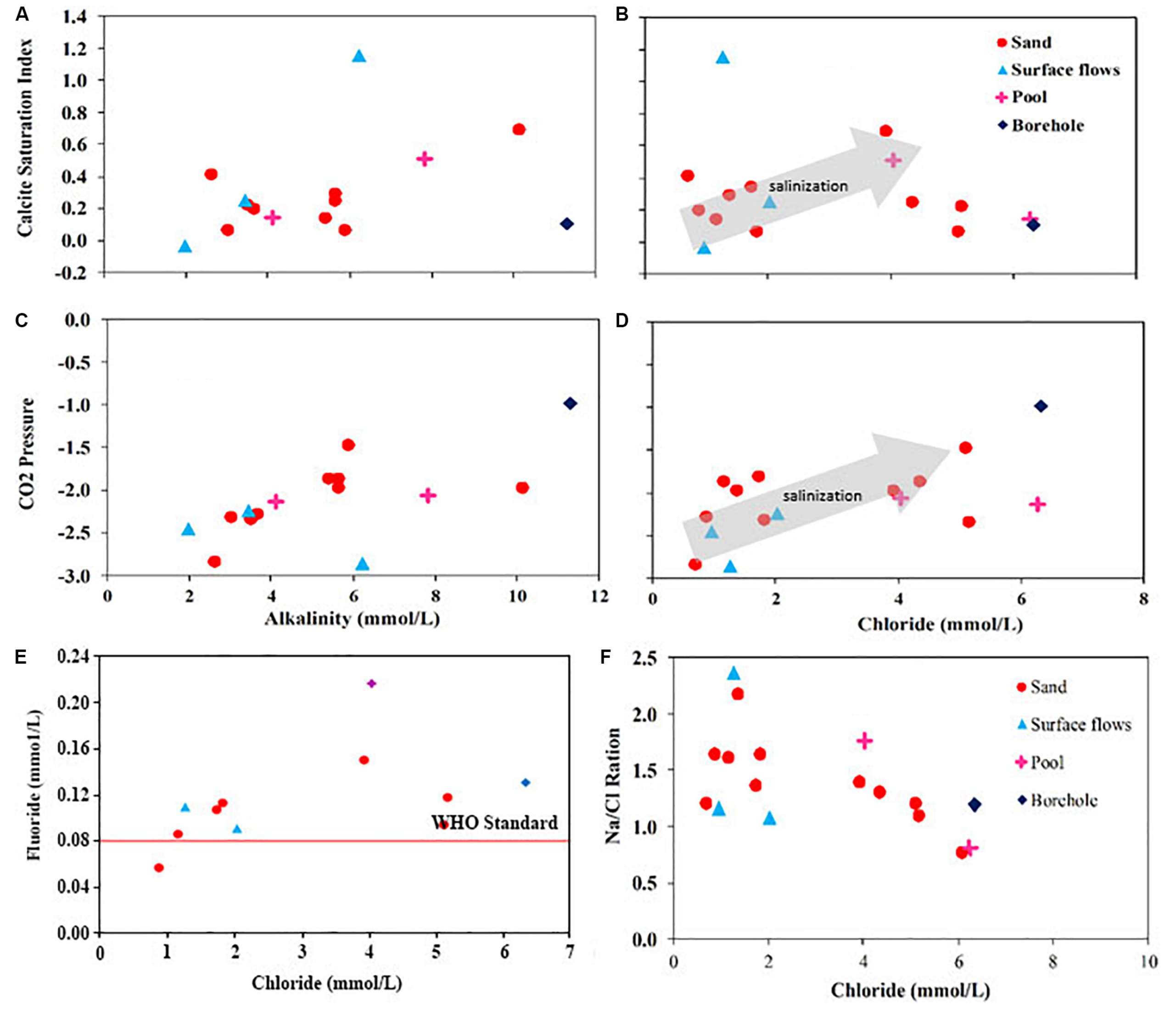

FIGURE 8 | Scatter plots for calcite saturation vs. alkalinity **(A)** and chloride **(B)**, CO2 pressure vs. alkalinity **(C)** and chloride **(D)**, fluoride vs. chloride **(E)** and Na/Cl ratio vs. chloride **(F)**.

are estimated as approximately 1.3 Mm^3/year. Sheep account for more than half the total livestock population in the Sand River sub-catchment, but water is also used by cows, goats and donkeys. In general, livestock accounts for 80% of the total water demand. Discrete isolated water bodies commonly referred to as water holes (Sheldon et al., 2010) were observed along sections of the river channel (**Figure 9**). Such water holes mainly occur at channel bends with a rocky river bed, in the vicinity of large riparian trees and channel sections with rock outcrops. Despite their shallow nature (<0.5 m), some of the water holes hold water through the dry periods. The drop in water level in the pool was similar to the drop in the sand deposits, suggesting a connection between the sand storage and the persistence of the water holes (**Figure 5D**). EC values for the sampled water holes ranged between 1,762 and 930 µS/m. A borehole in the vicinity of the sampled water holes had an EC value of 1,569 µS/m, while water from the alluvium nearby indicated an EC concentration of 975 µS/m.

Biota in the Sand River includes aquatic, semi-aquatic and terrestrial species (**Figure 10**). The water holes were observed to have fish particularly after a flow event. Tadpoles, mature frogs and turtles were also observed in most of the identified isolated water bodies along the Sand River. Unique though, are the amphibian species that burrow into the alluvium and stay above phreatic line through the dry spell (**Figure 10c**). Such species have the ability to go into a state of dormancy in which energy consumption is limited by reducing both the heart and respiratory rates. The Sand River has patches of undisturbed riparian vegetation in the upstream sections of the catchment. Roots of the vegetation penetrating the sand deposits were observed along the river channel (**Figure 10d**).

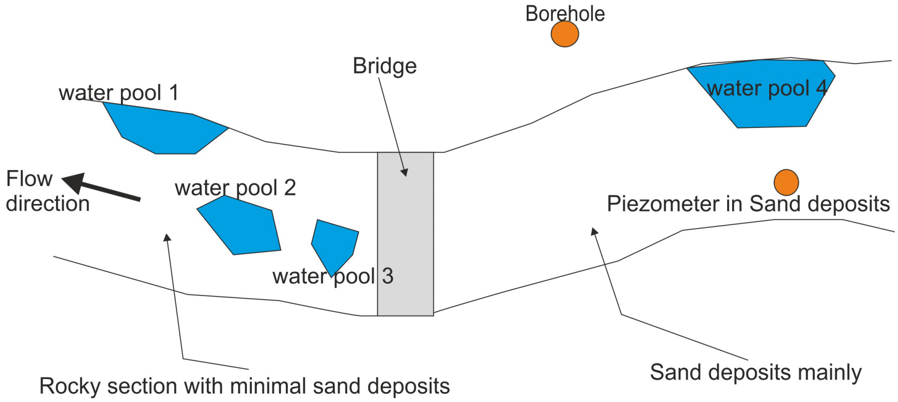

FIGURE 9 | Section of the Sand River studied to establish dependency of water holes on groundwater. The section is near Olderkesi Market Centre (**Figure 2**).

FIGURE 10 | Biota in the Sand River; **(a)** fish **(b)** turtle **(c)** frog commonly known as Spencer burrowing frog in Australia **(d)** roots of a riparian tree penetrating sand deposits through the water pool.

DISCUSSION

Results from the field show that variability in storm-related flood pulses in the Sand River is dependent on the antecedent soil moisture in the alluvium deposits underlying the river bed; similar to the characteristics illustrated by Pacheco-Guerrero et al. (2017) and Abdulrazzak and Sorman (2006). At the onset of a rainstorm, advancement of a surface flow wave downstream is limited by infiltration into the sand deposits. The rate of infiltration and percolation in comparison with the rate of flow of a flood governs the advance and magnitude of a flood on an unsaturated sand bed. As noted by Costa et al. (2013), the findings illustrate that groundwater recharge in the alluvial bed by transmission losses is an important function of water flow behavior in the Sand River. Even though observations in this research are based on only three storm events, limiting the extent to which concrete judgment on water flow behavior can be made, two critical observations are the time lag in the rising limbs and the similar behavior of the recession limbs. Rate of flow of a flood is a function of the rate at which run-off enters the river channel as well as the slope. On the other hand, infiltration rates are dependent on the properties of the sand deposits, including porosity. A flood cannot advance over an unsaturated sand bed if infiltration rates exceed the discharge rates. Thus, there is a lag in the rising limb of the surface water flow compared to the rising limb of the groundwater level (**Figure 5C**). Similar to our findings, Moulahoum (2018) also noted that logger data of the groundwater level in the Shashane riverbed aquifer, in the Mzingwane catchment, Zimbabwe, showed that the riverbed is entirely saturated at the beginning of the first major rainfall-runoff event and major surface runoff occurs only after the riverbed is saturated. Mansell and Hussey (2005) illustrated that flows in the sand deposits along sand rivers are an extension of surface discharges that can be estimated based on the flood water recession curve; an aspect that is further affirmed by the similar behavior characteristics of the recession limbs. However, the assumption may only hold until the saturation depth that corresponds to no surface flow conditions i.e., maximum depth of alluvium saturation on a dry riverbed. Saturation of this particular depth in which the groundwater recession limb is similar to the floodwater is dependent on the positive pressure exerted on the riverbed, usually equivalent to the flood height.

The water storage potential along the Sand River depends on the hydraulic properties of the alluvium as well as the geometry of the aquifer including the nature of the underlying layer. Wider sections of the river course have potentially larger sand volumes and thus a higher storage potential. The bedrock underlying alluvial deposits undulates, creating natural barriers that trap water upstream and therefore reduce lateral flows. Much of the water drawn from alluvial corridors in the dry periods is from these natural micro-reservoirs. Storage is replenished as the river is flooded a number of times in a hydrological year. Considering that a flood wave cannot advance over an unsaturated sand bed, each flow event that floods the entire river reach fully recharges the alluvial aquifer. Human settlements are located in the close vicinity to the river at a regular spacing of approximately 500 m. With an estimated combined domestic and livestock water demand of 1.3 Mm^3, the estimated daily water demand or required abstraction for every 500 m river stretch is 15 m^3/day. Considering the storage estimated for the sections A and B at full capacity varies between 13 and 17 m^3/m, the instantaneous storage volume likely ranges between 6,500 and 8,500 m^3 for each 500 m reach. Such storage volumes would meet demands for more than a year if it were assumed that it only supports domestic and livestock water demands. Given that the alluvial aquifer is replenished following each significant runoff event, this storage should be sufficient to meet the water requirements for livestock and human domestic demands with sufficient reserves to provide for wildlife and ecosystem sustainability. Nyongesa (2020), also noted that sand storage along ephemeral rivers can sufficiently support sustainable irrigated agriculture.

Besides artificial water abstraction from the alluvium along the Sand River, natural processes such as direct evaporation, transpiration by the riparian vegetation, seepage through fractured bedrock, and lateral flow accounts for continued decreases in stored water. Direct evaporation is evident from the deviation of the isotopic signature for the water in the alluvium from both the GMWL and LMWL. Gibson et al. (1993) noted that gradients for evaporation lines are always less than 8 but often fall between 4 and 6, where our line of fit lies. Although not investigated in this research, Hellwig (1973) and Love et al. (2011) found that evaporation occurs up to maximum depths of between 60 and 90 cm, depending on sand particle sizes. As a result, groundwater salinity tends to increase, as indicated by increasing Cl concentrations (Stigter et al., 1998). The chemistry of water in the sand storage is further affected by rock-water interactions, in a silicate rock environment where the chemical evolution of groundwater is mainly a function of residence time. The response of the alluvial system is fast; recharge rates and decreases in storage are rapid, which limits chemical evolution. However, the presence of micro-catchments allows storage of water under reduced evaporative effects long enough for sufficient interaction with the aquifer media. This is revealed by the higher ion contents, in particular Ca^{2+}, Na^{+} and HCO_3^{-}, as well as the presence of fluoride. The latter was present in concentrations above the drinking water guidelines, which needs to be considered when using the alluvial water for domestic supply.

Vertical losses through downward flow into fractured bedrock can also be an important loss of alluvial water, given that that once in the fracture zone it is more difficult to abstract the water. Groundwater level observations in the Sand River clearly showed that the rate of decline was larger than explained by evapotranspiration only (**Figure 5D**). Part of the decline can also be explained by lateral subsurface flow within the alluvial aquifer. Irrespective of the dominating process, such a decline has a direct impact on the storage capacity of the alluvial aquifer, especially when the sand layers are still relatively thin, as is the case here.

The Sand River is a linear oasis with a proliferation of woody vegetation along the riparian zone. Water storage in the alluvium ensures constant water availability for transpiration, thereby supporting the growth of riparian vegetation. Diurnal fluctuations observed from the groundwater level monitoring provides evidence of losses through transpiration (**Figure 6B**). Vegetation transpires maximally during the day. ET is almost negligible between midnight and 5:00 am (White, 1932). Observed increases in groundwater level when ET is negligible is an illustration of lateral flows in the alluvial deposits. The river hosts a range of aquatic (semi) and terrestrial organisms that are uniquely adapted to the "boom," "burst" and cease-to-flow hydrologic regimes (Sheldon and Thoms, 2008). Water holes along the river reach are hydrologically (semi)permanent features adapted to the dynamic inter-flood intervals thereby providing refugia to biota during no-flow conditions. Is persistence of the waterholes through dry periods dependent on water storage in the alluvium? Water level measurements coupled with water quality results during our study suggests that indeed, the isolated aquatic islands are alluvium groundwater storage dependent ecosystems.

Water storage along alluvial corridors of Sand Rivers is a shared resource between humans and natural ecosystems, and as such, both are susceptible to changes in use and availability patterns. Over-extraction of water from the alluvium may result to ecological stress particularly on water-controlled ecosystems. Such ecological stress becomes apparent through species migration, extirpation and shifts in the composition of riparian vegetation. For instance, unsustainable water resource development threatens persistence of waterholes thereby diminishing their capacity as refugia for both aquatic and semi-aquatic micro-organisms (Sheldon et al., 2010). Arnold et al. (2016) notes that a shift in vegetation composition can result to competitive species as opposed to more tolerant species adapted the flow variability of dryland rivers. The changes in vegetation types has been found to alter hydrological processes -such as evapotranspiration – controlling groundwater fluctuations or tip the water balance to either side – positive or negative (Poff and Zimmerman, 2010). On contrary, Moulahoum (2018), illustrated that water levels in the banks of Shashane Sand River in Zimbabwe sustaining the riparian corridors had the tendency to be higher, i.e., above the sand river water level, in the dry season, due to the finer texture and higher clay content. ERT measurements illustrated in **Figures 4A,B** also revealed a similar fine-textured and clay-rich sediments in the sub-surface. Such a phenomenon may enhance capillary rise to partly counteract the effects of the drop in water level in the sand river during the dry season caused by abstractions. Water resource exploitation along ephemeral rivers should thus be designed such that ecosystem integrity is preserved without limiting socio-economic water supply for the nearby communities.

CONCLUSION

We investigated water flow processes and storage potential along the Sand River using field-based measurements. Surface flow monitoring and measured groundwater level in the alluvium have shown that variability in flood magnitude is dependent on alluvium water saturation level. Advancement of a flood wave over unsaturated sand bed is dependent on the rate of infiltration and subsequent percolation, commonly referred to as transmission losses. However, other factors such as the slope of the river channel and rate of runoff flow into the channel play a key role in water flow behavior. Besides impacts on the flood behavior, transmission losses recharge the alluvial aquifer thus replenishing the nature-based water storage along the Sand River. Such storage is a critical alternative water source for communities along the river as it supports domestic use and livestock watering. We have made two critical observations with regard to flood behavior and groundwater recharge rates in the alluvium: (1) time lag in the rising limbs and (2) similar behavior in the recession limbs. Water storage in the sand deposits is also subject to losses due to natural processes such as direct evaporation, transpiration and lateral flow in the sand deposits. However, probing results at selected sections have also shown that bedrock underlying the alluvium undulates, thereby limiting lateral flows. The undulating nature creates micro-catchments that enhance storage to support water demands. Further, we have established that water storage in the alluvium also supports dependent ecosystems including riparian vegetation and water pools that act as refugia for (semi)aquatic biota. This research has demonstrated the potential of alluvial corridors along ephemeral rivers as alternative water sources for livelihood sustainability and rural community development in the water scarce arid (semi) regions of East Africa.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

SW designed the study, collected and analysed data and prepared the manuscript. TS, MM, and KF conceived the study, offered supervision on study design, data collection and analysis, funding and prepared the manuscript. LO and FO guidance on extended data analysis and prepared the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

The Dutch Organization for International Organization (NUFFIC) provided financial support for a study scholarship. The field data collection was funded by Mau Mara Serengeti (MaMaSe) Sustainable Water Initiative and The Netherlands Embassy in Kenya.

ACKNOWLEDGMENTS

We would like to acknowledge the financial support of the Dutch Organization for Internationalization in Education (NUFFIC) for the study scholarship that enabled this contribution. We are grateful in particular to the Mau Mara Serengeti (MaMaSe) Sustainable Water Initiative and the Netherlands Embassy in

Kenya for the generous financial support that enabled fieldwork activities. We further acknowledge the Kenya Water Resources Authority, Kericho Sub-regional office and the Olderkesi Water Resource User Association for providing support during the data collection. Many thanks to Professor Paul Shiundu for the opportunity to work within the Labs at the Technical University of Kenya for extended analysis of the data beyond the period of study.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00095/full#supplementary-material

FIGURE S1 | Frequency duration curve for the daily water level measured between July, 2013 and January, 2016 at the existing Gauge Location.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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in Environmental Science

ORIGINAL RESEARCH
published: 03 July 2020
doi: 10.3389/fenvs.2020.00080

Assessment of Greenhouse Gases Emission in Smallholder Rice Paddies Converted From Anyiko Wetland, Kenya

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Rice is an important food crop in Kenya and is the third most consumed cereal crop after maize and wheat. The high demand for rice has resulted in the conversion of wetlands to rice paddies and the increased use of fertilizer, ultimately reducing the ability of wetlands to store carbon. Consequently, emissions from wetlands of three potent greenhouse gases (GHGs): methane (CH_4), nitrous oxide (N_2O), and carbon dioxide (CO_2) have increased. This study assessed the influence of fertilizer application on GHGs emission, organic carbon and nutrient stocks in rice paddies in papyrus dominated wetlands in the Nzoia River basin in Kenya. Sampling was done on a weekly basis for the first two months, and thereafter twice per month in the Anyiko rice paddies, which is a smallholder system partly converted from the Anyiko wetland. Two replicates of three fertilization treatments (standard, control and under fertilization) were assigned randomly in six rice plots. The static chamber method was used to collect the GHGs, which were then analyzed using gas chromatography. Soil samples were collected and analyzed for nitrogen and organic carbon stocks. Statistical tests revealed no significant differences in organic carbon and nitrogen stocks among the three fertilization treatments. The mean CH_4 fluxes did not differ significantly among the three treatments where mean flux for control plots were 8.30 ± 4.79 $mgm^{-2}h^{-1}$; under-fertilized plots had a mean of 6.93 ± 2.42 $mgm^{-2}h^{-1}$ and standard fertilized plots mean fluxes were 4.00 ± 6.34 $mgm^{-2}h^{-1}$. Similarly, CO_2 mean fluxes were insignificantly different among the three treatments, where control plots had mean of 174.80 ± 26.81 $mgm^{-2}h^{-1}$, under-fertilized plots mean were 208.81 ± 36.20 $mgm^{-2}h^{-1}$ and standard fertilized plots mean fluxes were 248.29 ± 41.22 $mgm^{-2}h^{-1}$. However, mean N_2O fluxes were significantly different among the three treatments, control plots had a mean of -3.59 ± 2.56 $\mu gm^{-2}h^{-1}$, followed by under-fertilized with mean of -0.59 ± 0.45 $\mu gm^{-2}h^{-1}$ and standard fertilized plots with mean of 4.37 ± 3.18 $\mu gm^{-2}h^{-1}$. In this study, different fertilization scenarios had significant effects on N_2O emission but no significant effect on CO_2 and CH_4 emission, organic carbon and nutrient stocks. Therefore, there is need for sustainable use of wetlands to ensure a balanced role between ecosystem management and human services.

Keywords: rice paddies, wetland, fertilizer application, GHGs, climate change

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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *12 September 2019*
Accepted: *22 May 2020*
Published: *03 July 2020*

Citation:
Owino CN, Kitaka N, Kipkemboi J and Ondiek RA (2020) Assessment of Greenhouse Gases Emission in Smallholder Rice Paddies Converted From Anyiko Wetland, Kenya. Front. Environ. Sci. 8:80. doi: 10.3389/fenvs.2020.00080

INTRODUCTION

Wetlands occupy about 6% of the earth's surface; covering about 7% of Africa alone (Junk et al., 2013). In Kenya, wetlands cover ∼2.5% of the surface area of the country (14,000 km^2) and fluctuate up to 6% during rainy seasons (Crafter et al., 1992). Wetland drainage and land reclamation (conversion of wetlands to arable lands) for crop production, papyrus harvesting and draining of wastewater into the wetland have been reported to be the major threats leading to wetland degradation in Kenya (Morrison et al., 2012). Mironga (2005) also noted that drainage and conversion to arable land have been the key drivers to degradation of wetlands in Kenya.

Rice is one of the essential cereal crops grown globally, in Africa and in Kenya (Balasubramanian et al., 2007). The role of rice as a current and future global food security is inevitable since it is one of the three most important food crops globally after wheat and maize (FAO, 2016). The FAO (2017) predicts global rice production to reach 758.9 million tons (503.8 million tons, milled basis) by 2017. In Africa, 2016 season rice output records put the production at 30.8 million tons (20.1 million tons, milled basis) (FAO, 2017). In Kenya, rice cultivation was introduced in 1907 from Asia (Republic of Kenya, 2008). The annual rice consumption rate in Kenya is estimated at 548,000 metric tons whereas the annual production is 129,000 metric tons (Republic of Kenya, 2014). Rice is either grown in upland areas or in lowland areas where the fields are either rain fed or irrigated. Kenya's major irrigation schemes include Mwea, Yatta, Ahero, Bunyala, and west Kano. These schemes are operated by National Irrigation Board (NIB) and produce about 80% of the rice while the remaining 20% is produced from the rain fed fields (Republic of Kenya, 2008). The growing population and socioeconomic changes have stimulated the need for more agriculturally productive land in the pursuit to improve food security (Junk et al., 2013; Mitchell, 2013). To meet the high demand for rice caused by increasing population pressure, more natural wetland area is converted to rice paddies. This land conversion is coupled with an increased use of fertilizer to increase crop yield.

Global sources of GHG emissions are broadly categorized into natural (44.54%) and anthropogenic (55.46%) (Xi-Liu and Qing-Xian, 2018). Wetlands are natural sources of global GHGs emissions, and account for 17.2% of natural emissions. Olivier and Peters (2018) report that rice cultivation on flooded rice fields is the second largest anthropogenic source of CH_4 (10%) after cattle stocking. The same authors note that agricultural activities are the main source of N_2O where synthetic fertilizers (nitrogen content) account for 18% of N_2O emissions after cattle stocking (21%). Concentrations of GHGs in the atmosphere have been rising steadily since the industrial revolution (Olivier et al., 2017). Greenhouse gas emissions lead to climate change and this has been evidenced in the recent years through: rise in mean global temperature, decreasing snow and ice in the northern hemisphere, ocean warming, extreme weather conditions, and CO_2 concentration has increased by 40% since the pre-industrial era (Cubasch et al., 2013). An additional warming of 1.1°C to 6.4°C is anticipated by future climate change projections (NRC, 2010). To attain Sustainable Development Goal 13 (take urgent action to combat climate change), the 2015 Paris agreement on climate change requires member countries to reduce global warming to well below 2°C to combat climate change.

Rice paddies are an important source of GHG emission (Garthorne-Hardy, 2013). The main GHGs emitted from rice fields include CO_2, CH_4, and N_2O (Arunrat and Pumijumnong, 2017). The major processes responsible for production and emission of these GHGs are: oxic respiration (decomposition), methanogenesis, nitrification, and denitrification (Zhang et al., 2007). In paddy rice soils, CH_4 is produced through methanogenesis under anoxic conditions (Jain et al., 2004). Nitrous oxide production occurs through nitrification and denitrification processes under oxic and anoxic conditions, respectively, whereas, CO_2 production occurs when oxygen is supplied in the soil through decomposition process (Ishii et al., 2011). Rice paddy soils are usually waterlogged providing anoxic conditions; however, the soil can be supplied with oxygen at certain circumstances like when the paddy is drained, at the roots and at the soil-water interface thus providing oxic conditions.

Wetlands are usually waterlogged and therefore provide similar conditions as required in rice paddy soils. For that reason wetlands are converted to rice paddies. Draining of wetlands to convert them to agricultural land exposes soil organic matter to oxygen, leading to its oxidation and subsequent release as CO_2 to the atmosphere (Moomaw et al., 2018). Consequently, the ability of wetlands to sequester and store carbon is impaired and this leads to increased GHGs emission to the atmosphere, which contributes to climate change (Mitchell, 2013). Fertilizer application is one of the land management practices in rice paddies and is applied to increase crop yield (Singh and Singh, 2017). There are different fertilizer application management practices that influence the emission of GHGs for example: method of placement, type of fertilizer, level and form of fertilizer used (Linquist et al., 2012). Fertilizer application has been found to influence CH_4 and N_2O but have less impact on CO_2 emissions (Linquist et al., 2012). Wang et al. (2017) report that application of nitrogen fertilizer in rice paddies showed variability (increase or decrease) in CH_4 emissions but led to increase in N_2O emission. Generally, N fertilizer application increases the GWP of N_2O by 78% (Bin-feng et al., 2016). The nitrogen electron donors and acceptors can be nitrified or denitrified to N_2O when fertilizer is applied to the soil (Wang et al., 2017). Emissions of CO_2 from rice paddies is however low (<1%) since CO_2 emission is largely offset by primary productivity and atmospheric fixation by plants (Linquist et al., 2012). Apart from fertilizer application, farmers employ other management practices to increase yield production including clearing of natural wetlands to expand production area.

Studies on the effect of nitrogen fertilizer application on GHGs emissions in rice paddies have been conducted widely in other part of the world like in Asian countries (Shang et al., 2011; Cheng-Fang et al., 2012; Bin-feng et al., 2016; Arunrat and Pumijumnong, 2017). In sub-Saharan Africa, such studies remain limited despite considerable pressure on wetlands from agriculture particularly; smallholder farms (Houghton et al., 2012; Pelster et al., 2017). In Kenya for instance, area loss ranging from 34 to 55% have been reported in some wetlands in the last four to five decades majorly as a result of conversion to agriculture (Owino and Ryan, 2007; Ondiek et al., 2020). Due to alarming effect of global warming and climate change, understanding the effects of fertilizer applications in the areas of the wetland converted to agriculture is crucial. Therefore, this study assessed the effect of different fertilizer application scenarios on GHGs emissions in smallholder rice paddies converted from Anyiko natural wetlands in Kenya. The specific objectives of this study were to (1) compare soil organic carbon and nitrogen content in rice paddies under standard fertilization (basal, first and second topdressings), under-fertilization (first and second topdressings) and no fertilization (control); and (2) compare CO_2, CH_4 and N_2O emissions in rice paddies under standard fertilization, under-fertilization and no fertilization (control). We hypothesized that (1) different fertilizer application scenarios have no significant effect on the standing stocks of organic carbon and nitrogen in rice paddies; and (2) standard fertilization (basal, first and second topdressings) and under-fertilization (first and second topdressings) has no significant effect on CO_2, CH_4, and N_2O emission in rice paddies.

MATERIALS AND METHODS

Study Area

The study was carried in Anyiko irrigation scheme which is a smallholder system partly converted from Anyiko wetland located in North East Ugenya, Siaya County, Kenya (**Figure 1**). The irrigation scheme was established in 1977 by the Ministry of Agriculture and lies between longitudes 0°16', 38°56"E, 0°14', 18°66"E and latitudes 34°16', 35°55"N, 34°18', 0°57"N in Nzoia River Basin. Currently the scheme is managed by farmers. On inception, the scheme only used water diverted from the adjacent Anyiko wetland via a canal for irrigation. Over the years however, the farmers have converted parts of the wetland to rice paddies and several canals dug out for irrigation. The area of the scheme expanded as a result of conversion of the wetland is unknown. The area covered by the scheme is 120 acres with ∼100 farmers, each owning a paddy rice field of ∼¾ acres. The growing season of rice runs from April to December.

Study Design and Sample Collection

The study was carried out from September 2018 to January 2019, during rice growing season in Anyiko irrigation scheme. The experiment was completely randomized with two replicates of three treatments. The three treatments included different fertilization scenarios: standard fertilization (basal, first and second top dressings), under fertilization (first and second top dressings only), and control (no fertilization) at 50 kg of fertilizer per acre for each, excluding the control. Nitrogen Phosphorus Potassium (NPK) 23:23:0 was used for basal fertilization whereas calcium ammonium nitrate (CAN) was used for first and second top dressings. Basal application was done immediately after transplanting, first top dressing was done 21 days after transplanting (DAT) and second top dressing was done 45 DAT. The fertilizer was applied using broadcasting method. In each of the six study plots, three gas chambers were placed. Gas samples were collected and analyzed (see section Study Design and Sample Collection) as well as soil samples (see section Soil Sampling and Analyses for NH4-N, NO3-N, TN and OC).

Gas Sampling and Analysis for CO_2, CH_4 and N_2O Fluxes

Greenhouse gases, CO_2, CH_4 and N_2O fluxes were measured on a weekly basis for the first two months, and thereafter twice a month in the rice paddies using the static chamber method (Butterbach-Bahl et al., 2016). The chambers were fabricated from twenty-four 30-liter plastic buckets from which eighteen were used for bases (34 cm diameter × 15 cm height) and six as lids (34 cm diameter × 23 cm diameter × 41 cm height). The plastic buckets were used because they are inert to the gases being sampled (Collier et al., 2014). The lids were fitted with a gas sampling port, thermometer to measure chamber internal temperature and 50 cm long vent tube (2.5 mm diameter) to equilibrate pressure differences between ambient and headspace as indicated in **Plate 1** (Collier et al., 2014; Rosenstock et al., 2016; Pelster et al., 2017; Tully et al., 2017). The lids were also insulated with a reflective duct tape all round to minimize insulation. Three chamber bases per rice plot of about a quarter of an acre were inserted 10 cm into the soil 1 week before the first gas sampling. The chamber bases remained in the field for the entire sampling period to prevent collection of GHGs emitted due to soil disturbances **(Plate 2A)**.

During each sampling event, the gas samples were collected between 10 am and 12 noon since studies have shown that this gives average daily emissions estimates (Butterbach-Bahl et al., 2016). Given the six rice plots and having to conduct the sampling within the given time frame, two people (1 person per rice plot) collected the gas samples. Hence, three lids per person per rice plot were used during the gas sampling. The bases and lids were clamped together for 30 min using metallic clips and a rubber seal fitted between them to ensure airtightness (Rochette, 2011). The chambers covered at least 4 rice plants in a transplanted system with spacing of 4 by 6 inches (Butterbach-Bahl et al., 2016). Gas samples (60 ml) were collected from the headspace at 0, 10, 20 and 30 min after lids deployment using a propylene syringe fitted with Luer lock, therefore, giving a total of 4 gas samples per rice plot (**Plate 2B**). The air inside the chamber was manually mixed before gas collection at each time interval by drawing gas from the chamber then pumping it back several times. To overcome spatial heterogeneity of soil GHG fluxes, samples were pooled from the three replicate chambers at each plot to form a composite air sample of 60 ml (Arias-Navarro et al., 2013). The first 40 ml of the sample was used to flush a 10 ml sealed glass vial through a rubber septum, while the final 20 ml was pushed into the vial, leading to a slight overpressure to minimize leakage and contamination of the gas with ambient air (Rochette and Normand, 2003). The ambient air sample was collected using the same procedure in order to assess ambient GHGs concentration during sampling. The height of each chamber base was measured on each sampling date to derive the total chamber volume (volume of the lid = 30 liters plus volume of the base = base area × height). The gas samples were wrapped with parafilm over the vial's crimp seal and transported to the International Livestock Research

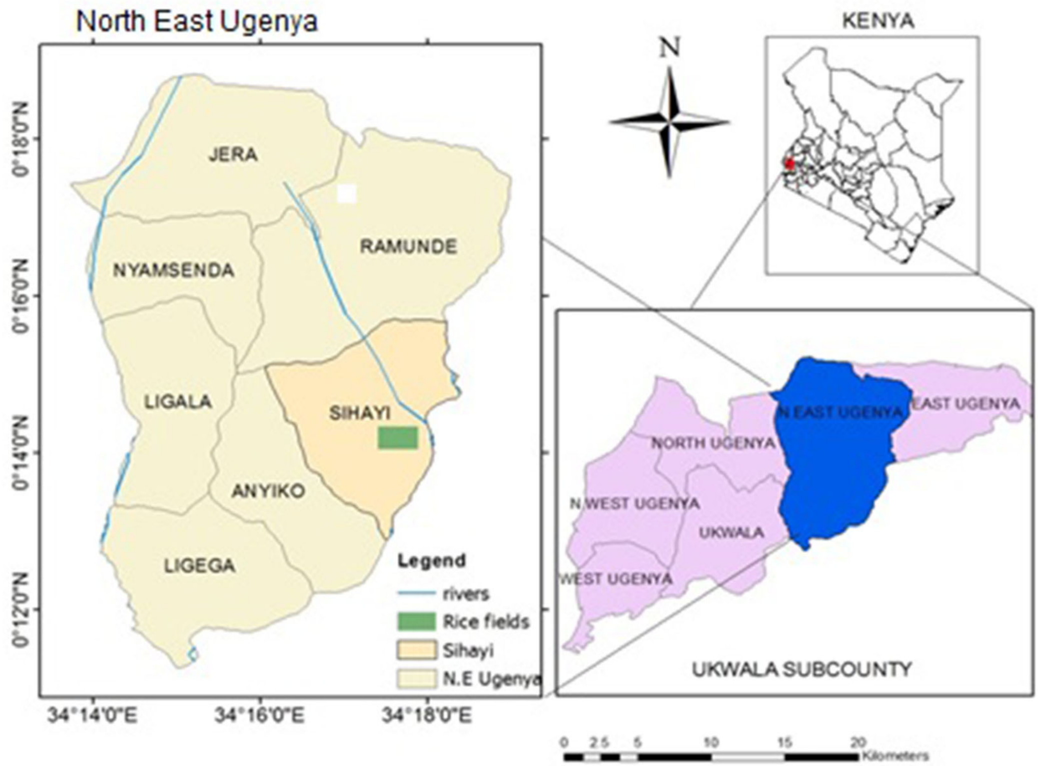

FIGURE 1 | Map of Kenya showing the location of Anyiko rice fields (Modified from Topographical map of Kenya, scale 1:50,000).

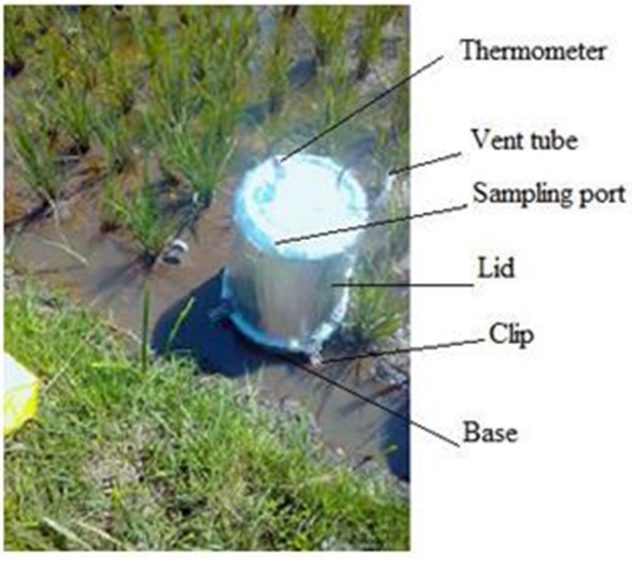

PLATE 1 | Pictorial representation of a fabricated gas chamber.

Institute (ILRI) laboratory, in Nairobi for analysis within 12 h after collection.

The gas samples were analyzed for CO_2, CH_4, and N_2O in an SRI 8610C gas chromatograph (2.74 m Hayesep-D column) fitted with a 63Ni-electron capture detector for N_2O and a flame ionization detector for CH_4 and CO_2 (after passing the CO_2 through a methanizer) (**Plate 3**). The flow rate for the carrier gas (N_2) was 20 mL min^{-1}. Gas concentrations were calculated based on the peak areas measured by the gas chromatograph relative to the peak areas measured for four standard calibration gases. The ideal gas law, atmospheric pressure, internal chamber temperature and chamber volume, measured during sampling were then used to convert the concentrations to mass per volume flux calculated using the the equation below (Butterbach-Bahl et al., 2011).

$$\text{Flux}_{\text{GHG}(\text{mgm}^{-2}\text{h}^{-1})} = \text{Ct} \times \left(\frac{\text{M}}{\text{Vm}}\right) \times \left(\frac{\text{V}_{\text{ch}}}{\text{A}_{\text{ch}}}\right) \times \left(\frac{273.15}{273.15+\text{t}}\right) \times \text{P} \times 60 \quad (1)$$

Where: Ct = slope derived from the linear regression (ppm min^{-1}) for CH_4 and CO_2 and (ppb min^{-1}) for N_2O-N, M = molar weight (g mol-1) (C = 12 for CH_4 and CO_2, and N = 28 for N_2O), Vm = molar gas volume ($m^1 mol^{-1}$), (22.41), Vch = Volume of the chamber headspace (3 0 liters), A_{ch} = Area of gas chamber, t = Chamber temperature (°C), P = Pressure at the time of sampling (atm), 60 = conversion factor of minutes to hour.

Auxiliary Measurements

During each gas sampling campaign, soil temperature at a depth of 0 to 20 cm was measured in each rice plot

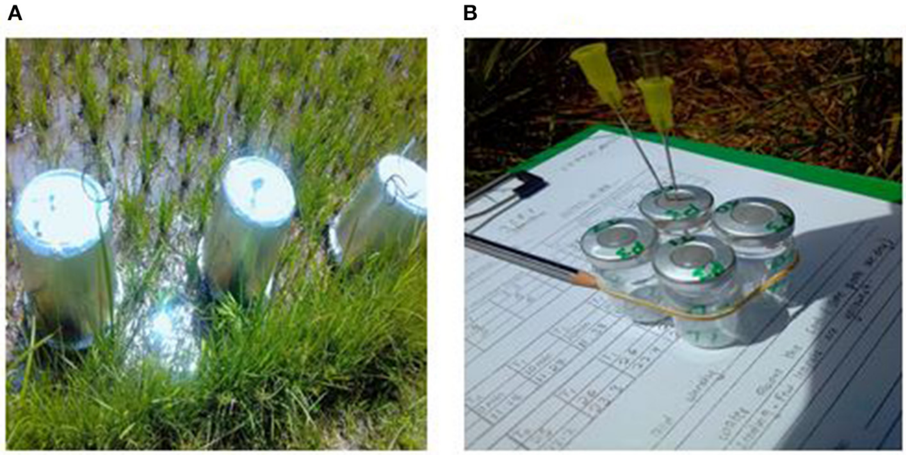

PLATE 2 | (A) Shows the three chambers installed in a plot, **(B)** pre-labeled 10 ml glass vial with crimp seal fitted with two syringes, one for evacuation and one for refilling the vial.

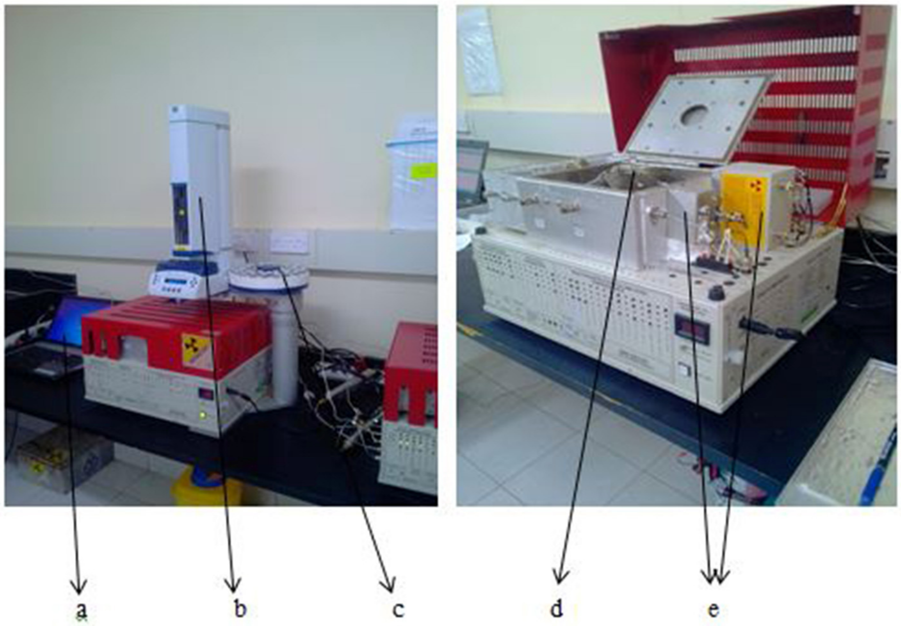

PLATE 3 | (a) A computer for recording peaks, (b) automated injector, (c) gas sample tray, (d) separation columns, (e) the detection units (FID and ECD).

using digital thermometer (Brannan). Digital thermo-hygrometer (model 1141Y43) was used to measure air temperature. Bulk density was determined on the upper 0 to 15 cm using the bulk density ring (98 cm^3). Atmospheric pressure was measured during each sampling campaign using a barometer (installed in phone), though the pressure was quite constant since altitude did not change.

Soil Sampling and Analyses for NH_4–N, NO_3-N, TN and OC

Soil samples were collected using random composite sampling technique at each rice plot using soil auger to a depth of 0 to 15 cm. The samples were collected on every sampling campaign for soil moisture, NO_3-N and NH_4-N analysis. For soil OC and TN analysis, sampling was carried out twice per month. The samples were then transferred into polythene bags and placed in a cool box containing ice packs for transportation to the laboratory for further analysis.

The standard procedure described by Okalebo et al. (2002) was followed to determine soil moisture content. Soil moisture was determined by oven-drying 250 g of soil samples from each rice plot for 48 h at 105°C and then reweighed. Soil moisture content was calculated as:

$$\text{Soil moisture content (\%)} = \frac{\text{weight of the moisture} \times 100}{\text{weight of the dry soil}} \quad (2)$$

The concentrations of NO_3-N and NH_4-N in the soil samples were determined by colorimetric method, where 10 g of fresh soil samples were extracted with 100 ml of 0.5 M K_2SO_4. The solution was shaken for 1 h on a Gallenkamp orbital shaker. The samples were filtered through Whatman GF/C filters and the supernatant analyzed for NO_3-N and NH_4-N. The concentrations of NH_4-N and NO_3-N were calculated from their respective equations generated from standard calibration curves. The concentrations were converted to soil mass as follows:

$$\begin{aligned} & \mathrm{NH_4^+}\left(\mu\mathrm{g\,kg^{-1}}\right)/\mathrm{NO_3^-}\left(\mu\mathrm{g\,kg^{-1}}\right) \\ & = \frac{\left(\mathrm{a}-\mathrm{b}\right) \times \mathrm{V} \times \mathrm{MCF} \ \times \mathrm{f} \ \times 1000}{\mathrm{w}} \end{aligned} \quad (3)$$

Where a = concentration of N in the solution, b = concentration of N in the blank, v = volume of the extract; w = weight of the fresh soil; MCF = moisture correction factor; f = dilution factor.

Total nitrogen was determined by Kjeldahl method (acid digestion, followed by steam distillation and then titration). Soil was oven dried (70°C) and from the dried sample, 0.3 g was digested using 2.5 ml of digestion mixture (hydrogen peroxide, sulphuric acid, selenium, and salicylic acid) at 360°C for 2 h. Thereafter, an aliquot of 10 ml was transferred into a reaction chamber. This was followed by addition of 10 ml of 1% sodium hydroxide and immediately steam distilled for 2 min into 5 ml of 1% boric acid. The distillate was titrated with N/140 HCl until endpoint (color change from green to definite pink). Concentration of total nitrogen was calculated as follows:

$$\text{\% N in soil sample} = \frac{\mathrm{b} - \mathrm{a} \times 0.1 \times \mathrm{v} \times 100}{1000 \times \mathrm{w} \times \mathrm{al}} \quad (4)$$

Where a = volume of the titer HCL for the blank, b = volume of titer HCL for the sample, v = final volume of the digestion, w = weight of the sample taken and al = aliquot of the solution taken for analysis.

Organic carbon was determined by Walkley–Black method [digestion by sulphuric acid and aqueous potassium dichromate ($K_2Cr_2O_7$) mixture] (Okalebo et al., 2002). Soil samples was oven dried (70°C) to a constant weight. This was followed by complete oxidation of 0.3 g using 7.5 ml sulphuric acid and 5 ml aqueous potassium dichromate ($K_2Cr_2O_7$) mixture. The unused $K_2Cr_2O_7$ was titrated against ferrous ammonium sulfate to endpoint where color changed from greenish to brown. Difference between the added and residual $K_2Cr_2O_7$ gave the measure of OC content in soil. The concentration of OC was determined according to Okalebo et al. (2002).

TABLE 1 | Ancillary variable affecting GHG emissions measured at the study site.

Treatment	Density (g/ml)	Moisture content (%)	Soil temperature (°C)
Control	0.95 ± 0.15^a	53.93 ± 14.97^a	23.99 ± 1.27^a
Under	1.01 ± 0.18^a	74.72 ± 18.55^b	22.95 ± 1.33^a
Standard	1.04 ± 0.17^a	69.14 ± 18.17^{bc}	23.43 ± 1.60^a

Values are presented as mean ± standard deviation. Similar letters indicate no significant difference whereas different letters indicate significant differences.

$$\text{Organic Carbon (\%)} = \frac{\left(0.003 \times 0.2\left(\mathrm{Vb} - \mathrm{Vs}\right) \times 100\right)}{\mathrm{w}} \quad (5)$$

Where Vb = volume in ml of 0.2 M ferrous ammonium sulfate used to titrate reagent blank solution, Vs = volume in ml of 0.2 M ferrous ammonium sulfate used to titrate sample solution and 12/4000 is the mili-equivalent weight of C in grams.

Data Analysis

Data collected were statistically analyzed using IBM SPSS statistics version 2.0 (USA). All tests were carried out at $p < 0.05$ significance level and data subjected to normality (Shapiro-Wilk) and homogeneity of variance (Levene's) tests. Data for soil organic carbon and total nitrogen were normality distributed and therefore, one-way ANOVA was used to test significant differences between means of their standing stocks in the different treatments. The data for NH_4-N, NO_3–N and fluxes of CH_4, CO_2, and N_2O were not normally distributed and therefore analyzed using the non-parametric Kruskal–Wallis test. Under different fertilizer application scenarios, only N_2O emission varied significantly and hence, Tukey's *post hoc* test was applied to separate the means. Spearman's rank correlation was conducted to determine the relationship between soil properties (C/N ratio, soil moisture content, organic carbon, total nitrogen) and GHGs.

RESULTS

Study Site Characteristics

The mean air temperature and soil temperature for the site were 27.06 ± 3.32°C and 23.46 ± 1.45°C, respectively (**Table 1**). The soil moisture content differed significantly within the plots [one-way ANOVA, $F_{(2,\,57)} = 7.74$ $P = 0.001$] with control plots recording lower moisture content (53.93 ± 3.35%) compared to standard fertilized plots (69.14 ± 4.06%) and under-fertilized plots (74.72 ± 4.15%) (Tukey's *post-hoc* test $P < 0.05$) (**Table 1**). The soil bulk density showed no significant variations among the sites [one-way ANOVA $F_{(2,\,57)} = 1.697$, $P = 0.192$].

Comparison Between Soil Organic Carbon and Nitrogen Content Among Fertilization Scenarios

Mean TN for the control plots was 0.70 ± 0.38%, 0.78 ± 0.43% for under-fertilized and 0.71 ± 0.35% for standard fertilized plots. The mean soil organic carbon fluxes did not differ significantly among the three treatments [one-way ANOVA, $F_{(2,33)} = 0.219$, $P = 0.804$; **Figure 2**, left]. The mean organic carbon for the control plots was 2.21 ± 0.70%, for the under-fertilized was 2.26 ± 0.68% and for the standard fertilized plots 2.08 ± 0.64%. Mean TN also did not differ significantly among the three treatments (one – way ANOVA, $F_{(2, 33)} = 0.134$, $P = 0.875$; **Figure 2**, right). Mean soil NH_4-N for control plots was 44.96 ± 9.60 μg/Kg, 63.57 ± 10.28 μg/Kg for standard fertilized plots and 68.02 ± 12.49 μg/Kg for under-fertilized plots (**Figure 3**, left). Mean soil NH_4-N however did not differ significantly among the three treatments (Kruskal–Wallis test, $P = 220$). Similarly, mean NO_3-N was also insignificant among the three treatments (Kruskal–Wallis test, $P = 0.602$). Control plots had a mean of 49.37 ± 18.82 μg/Kg, 63.64 ± 26.20 μg/Kg for under-fertilized plots and 71.66 ± 29.44 μg/Kg for standard fertilized plots (**Figure 3**, right). The C/N ratio did not differ significantly among the three treatments [one-way ANOVA, $F_{(2, 33)} = 0.399$, $P = 0.674$]. The C/N ratio for the control plots ranged from 1.2:1 to 8.0:1, under-fertilized plots ranged from 1.3:1 to 8.0:1 while that for standard fertilized plots ranged from 1.2:1 to 5.7:1.

Carbon nitrogen ratio (C/N), TN, organic carbon and soil moisture were determined as some of the drivers of GHG emissions using Spearman correlation. Carbon/nitrogen ratio affects GHGs emissions by influencing mineralization and immobilization processes of the soil. Nitrous oxide showed positive correlation with TN but negative correlation with organic carbon (OC) and C/N ratio; However, both the positive and negative correlations were statistically not significant (**Table 2**). Methane showed an insignificant positive correlation with OC, C/N ration and TN (**Table 2**). Carbon dioxide showed an insignificant positive correlation with OC and C/N ration whereas it had a negative correlation with TN which was equally not significant. Total nitrogen and C/N ratio showed a significant negative correlation ($r_s = -0.808$) whereas OC and C/N ration had a significant positive correlation ($r_s = 0.370$), as illustrated in **Table 2**. However, there was no significant correlation between the soil moisture and the GHGs as shown in **Table 2**.

Comparison of GHG Fluxes Among the Fertilization Scenarios

The mean CH_4 flux was slightly lower in the under-fertilized plots (7.80 ± 2.12 $mgm^{-2}h^{-1}$) compared to that of standard fertilized (10.68 ± 3.79 $mgm^{-2}h^{-1}$) and control (10.82 ± 3.74 $mgm^{-2}h^{-1}$) plots. No significant difference in the CH_4 fluxes was observed among the fertilization scenarios (Kruskal–Wallis test, $P = 0.964$) as shown in **Figure 4**. No significant differences in mean CO_2 flux were observed among the three fertilization scenarios (Kruskal–Wallis test, $P = 0.573$; **Figure 4**). The mean carbon dioxide (CO_2) flux was slightly higher in the standard fertilized plots (248.29 ± 41.22 $mgm^{-2}h^{-1}$) compared to that of the under fertilized plots (208.81 ± 36.20 $mgm^{-2}h^{-1}$) and control plots (174.80 ± 26.81 $mgm^{-2}h^{-1}$). The mean N_2O flux was significantly higher in standard fertilized plots (4.37 ± 3.18 $\mu gm^{-2}h^{-1}$) than in the control plots (−3.59 ± 2.56 $\mu gm^{-2}h^{-1}$), (Tukey's *post-hoc* test, $P = 0.009$). However, there was no statistical difference in the mean N_2O fluxes between standard fertilized plots and under-fertilized plots with a mean of −0.59 ± 0.45 $\mu gm^{-2}h^{-1}$, (Tukey's *post-hoc* test, $P = 0.140$; **Figure 4**). The mean N_2O fluxes in control and under-fertilized plots also had no statistical difference (Tukey's *post-hoc* test, $P = 0.260$; **Figure 4**). The mean GHG fluxes indicated that under-fertilized rice plots were a sink for N_2O (−0.59 ± 0.45 $\mu gm^{-2}h^{-1}$) and a source for CH_4 (6.93 ± 2.42 $mgm^{-2}h^{-1}$) and CO_2 (208.81 ± 36.20 $mgm^{-2}h^{-1}$). Standard-fertilized rice plots were source for N_2O (4.37 ± 3.18 $\mu gm^{-2}h^{-1}$), CO_2 (248.29 ± 41.22 $mgm^{-2}h^{-1}$) and CH_4 (4.00 ± 6.34 $mgm^{-2}h^{-1}$). The control rice plots acted as sink for N_2O (−3.59 ± 2.56 $\mu gm^{-2}h^{-1}$) and a source for CH_4 (8.30 ± 4.79 $mgm^{-2}h^{-1}$) and CO_2 (174.80 ± 26.81 $mgm^{-2}h^{-1}$).

Global warming potential of CH_4 and N_2O were estimated by multiplying their fluxes by the IPCC global warming potentials factors which are 25 and 298, respectively, Solomon et al. (2007), and thus converting into CO_2 equivalents. The combined effect of the three treatments combined on greenhouse gases emission summed up in the mg CO_2 equivalents (CO_2 E) did not show any statistical difference (**Table 3**). The total effect for the three treatments after applying the CO_2 equivalents was not significantly different (Kruskal–Wallis test, $P > 0.05$).

DISCUSSION

Carbon and Nitrogen Stocks in Rice Paddies

Wetland based rice production is an important source of GHGs (Garthorne-Hardy, 2013; Wang et al., 2017). Increased conversion of wetlands to rice paddies reduces their ability to store carbon, thus increasing amount of GHGs (Mitchell, 2013). In this study, low levels of organic carbon stocks were recorded throughout the study period as indicated by the results. Drainage of wetland and land preparation for rice plantation exposed the accumulated organic carbon to oxygen and this accelerated oxidation of organic matter to CO_2 and thus reduced carbon stocks. Kumar et al. (2014) and Ma et al. (2016) reported loss of organic carbon through cultivation and wetland drainage, which could be an explanation for the low levels of organic carbon observed in this study. Mitsch and Hernandez (2013) also noted that drainage of saturated wetland soils in addition to its natural dryness result in increased oxygen diffusion, translating to higher rates of decomposition of organic carbon, consequently an increase in CO_2 emissions. The observed low soil organic carbon can also be attributed to the high CO_2 emission in all the three fertilization scenarios. According to VandenBygaart et al. (2003), when soils in a natural state are converted to agricultural land, there is an important loss of soil organic carbon (SOC) mainly in the form of CO_2. Furthermore, rice paddies are characterized with anoxic conditions which result in methanogenesis, leading to a loss of carbon as CH_4 and hence reduce carbon stocks (Jain et al., 2004). The loss of soil organic carbon in Anyiko rice paddies can also be explained by–alternate drying and wetting conditions which favor growth of microorganisms and hence high carbon mineralization (Ma et al., 2017). Other studies have also reported an increase in soil microbial activity and carbon mineralization under alternate drying and wetting conditions in

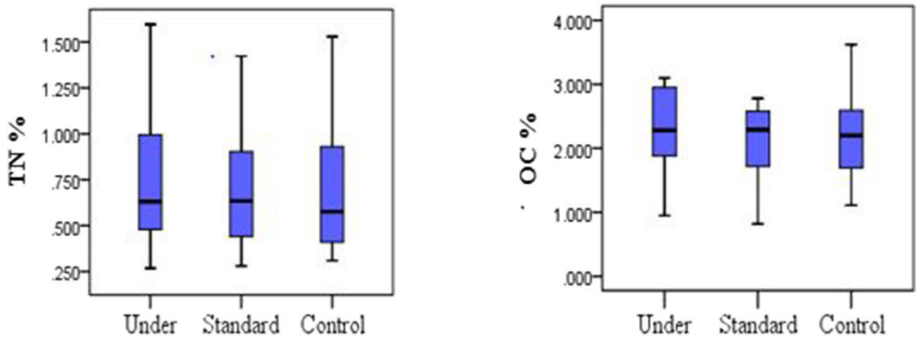

FIGURE 2 | Comparison between nitrogen and carbon stocks in the soil under different fertilizer treatments, (One-way ANOVA, $P > 0.05$).

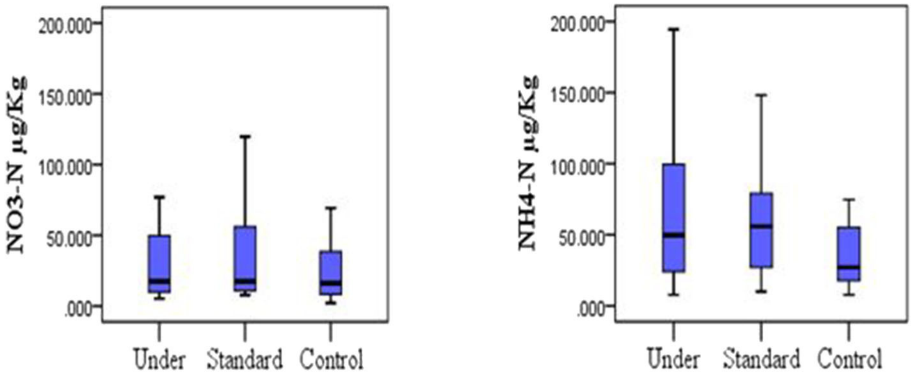

FIGURE 3 | Distribution of nitrogen species (nitrate and ammonium) under different fertilization scenarios in the soil, (Kruskal-Wallis test, $P > 0.05$).

incubation experiments (Fierer and Schimel, 2002; Zhao et al., 2011). The alternate drying and wetting season experienced during the experiment supplied more oxygen into the soil and hence increased oxidation of soil organic carbon which results to high emission of CO_2 into the atmosphere.

The two major microbial processes responsible for nitrogen transformations in soil are mineralization and assimilation by plants and microorganisms (Booth et al., 2005). In this study, the amount of total nitrogen increased from the initial value recorded in pretest (0.18 ± 0.06%) to 0.73 ± 0.38% after the experiment. Supply of nitrogen fertilizer in the soil during the experiment led to increased nitrogen stocks in under-fertilized and standard fertilized plots. Even though the amount of total nitrogen increased, the effect of the different treatments on the plots was not significant. According to Fuhrmanna et al. (2018), accumulation of nitrogen in the soil could be due to immobilization and retention of N fertilizer in the soil. The applied nitrogen fertilizer increased the available nitrogen stock but did not affect the amount of NH_4-N and NO_3-N among the three fertilizer application scenarios used. However, the standard fertilized and under-fertilized plots had high amount of NH_4-N and NO_3-N compared to control plots. This could be associated with fact that application of N fertilizer supplied more nitrogen substrate resulting to enhancement of mineralization and ammonification process (Chirinda et al., 2018). Consequently, more ammonium in the fertilized plots than in the control plots, though the impact was not substantial. Lowland rice is usually grown in waterlogged soils and this condition leads to reductive deamination (conversion of amino acid-N to ammonia via saturated acids), a process called ammonification (Sahrawat, 2010). Additionally, due to varying weather conditions at the study site, the field experienced episodic dry and wet periods. During dry periods, soils become relatively aerated and ammonium formed during mineralization got converted to nitrate via nitrite under oxic conditions (nitrification) (White and Reddy, 2001). This can explain the observed high amount of NO_3-N in the paddy soil. Also Sahrawat (2010) noted that nitrification can be supported at the rice plant's root-soil interface in wetland soils by oxygen transported through the air spaces or aerenchyma tissues of the stem and roots of the plant.

The ratio of carbon to nitrogen (C/N) in arable soils usually ranges between 8:1 and 15:1, with the median being 10:1 and 12:1 (Brady and Weil, 2008). The C/N ration in this study ranged between 1:1.2 and 8:1 which is quite low compared to the normal range of 8:1 and 15:1. Carbon nitrogen ratio in the soil is very important because it affects mineralization and immobilization processes of soil. The available carbon and nitrogen stocks in

TABLE 2 | Correlation matrix between GHGs, organic carbon, total nitrogen and carbon-nitrogen ratio.

Parameters		N_2O	CH_4	CO_2	OC	TN	C/N	MC
N_2O	r_s	1.000						
	Sig							
CH_4	r_s	**−0.395****	1.00					
	Sig	0.002						
CO_2	r_s	0.004	0.050	1.000				
	Sig	0.976	0.703					
OC	r_s	−0.153	0.159	0.054	**1.000**			
	Sig	0.374	0.354	0.755				
TN	r_s	0.046	0.016	−0.005	0.192	1.00		
	Sig	0.791	0.928	0.977	0.262			
C/N	r_s	−0.149	0.123	0.030	**0.370***	**−0.808****	1.000	
	Sig	0.387	0.476	0.860	0.027	0.000		
MC	r_s	−0.166	0.180	0.100	0.940	−0.027	0.017	1.000
	Sig	0.206	0.168	0.448	0.585	0.878	0.923	

**Correlation is significant at 0.05. **Indicate significance at 0.01. The bold values indicated where significant correlation was observed between the variables.*

soil, deposition from the atmosphere, addition of manure and application of inorganic fertilizer influences the GHGs emissions (Oertel et al., 2016). This study noted that N_2O emissions increased with decreased C/N ratio but CH_4 and CO_2 had a positive correlation with C/N ratio, though not significant. This is in agreement with the study by Oertel et al. (2016) who reported a negative correlation of N_2O emission with the C/N ratio, with the lowest emission being recorded at C/N $\geq$ 30 and highest at C/N values of 11 and a positive correlation of CO_2 and CH_4 emission with the C/N ratio. Toma and Hatano (2007) noted that, N_2O and CO_2 emissions increased as the C/N ratio decreased, but not significantly. It is worth noting that in this case, the result for CO_2 contradicts the results of the study by Oertel et al. (2016) and the results of this study. Moreover, intensive management of the peat lands has been found to alter the soil C/N balance, leading to higher variability of GHG emission (Veber et al., 2017).

Other environmental and agronomic factors like temperature, soil moisture content, water regimes, pH, C:N ratio, nutrient supply among others affect the mineralization processes in waterlogged rice soils (White and Reddy, 2001; Li et al., 2003). The observed high NO_3-N content compared to NH_4-N could be because of varying environmental factors during the experiment, like water regime. Sahrawat (2008) explained that mineralization of organic nitrogen in aerobic soils resulting to formation of NO_3-N (nitrification) is more sensitive to high temperature than ammonification. However, more studies need to be done to investigate the impact of environmental and agronomic factors to nitrification and ammonification.

Greenhouse Gas Fluxes Under Different Fertilizer Application Scenarios

Greenhouse gas fluxes for CH_4 and CO_2 were not significantly affected by fertilizer application regimes. N_2O fluxes however varied significantly among the three treatments. This suggests that whether there was fertilizer input or not, the wetlands soils had adequate carbon stocks for the production of GHGs, particularly CH_4 and CO_2. Application of NPK 23:23:0 and CAN at a rate of 50 kg per acre at planting and for top dressing, respectively, promotes release of N_2O as opposed to when fertilizer is applied only at planting or no fertilizer used at all.

Methane emissions in flooded paddy rice fields or any waterlogged soils occur due to anoxic conditions (Ma et al., 2010). The emissions of CH_4 to the atmosphere from paddy rice fields constitute a predominant source of anthropogenic CH_4 (Agnihotris et al., 1998). The three fertilization scenarios did not have an effect on the amount of CH_4 emission. This is in consistent with a study done by Linquist et al. (2012), which reported no effect of fertilizer N rate on CH_4 emissions. Even though CH_4 emission was not affected by the varying fertilization scenarios, the general CH_4 emissions from all the treatment plots were high. The consistently high soil moisture content created by the hydrologic modification to suit rice production provided favorable conditions for methanogens which proliferate methanogenesis (Veber et al., 2017). Lu et al. (2000) explained that fertilized larger plants provide more carbon substrate (roots and exudates) for methanogens thus enhances CH_4 production. Fertilization also leads to enlarged aerenchyma in rice plants and therefore enhancing the pathway for gas movement through the soil substrate and consequently facilitates CH_4 emission (Tang et al., 2018). Nitrogen fertilizer applications however, have been reported to have varying effects on CH_4 emissions. Shang et al. (2011) reported stimulation of CH_4 emission with N fertilizer application. According to Venterea et al. (2005) CH_4 emission is inhibited with N fertilizer application and in certain situations there are no significant effects of different N fertilizer application regimes on CH_4 emission (Mosier et al., 2006).

Fertilizer application regime did not affect the CO_2 emissions. Since fertilizer application had no direct effect on carbon stocks, therefore under similar humidity conditions, a difference in organic carbon based GHG emission is not expected. Carbon dioxide emissions to the atmosphere occur under oxic conditions which favors microbial decomposition of organic matter

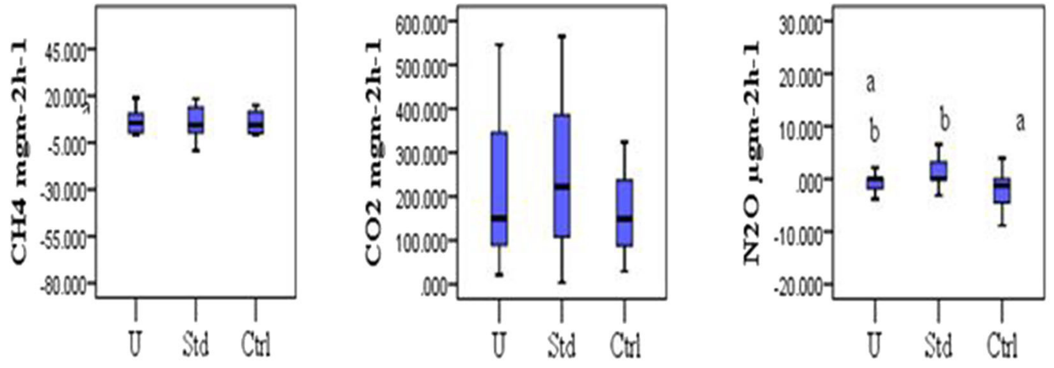

FIGURE 4 | Comparison of GHG fluxes (CH_4 mgm^{-2}h^{-1}, CO_2 mgm^{-2}h^{-1}, and N_2O mgm^{-2}h^{-1}) among the three fertilization scenarios (U, Under-fertilized; Std, Standard fertilized; Ctrl, Control). Different letters denote significant difference, while similar letters indicate no significant differences (Kruskal Wallis test, $P > 0.05$). Pairwise comparison indicated that the significant difference was between control and standard fertilization.

TABLE 3 | Total effect of the greenhouse gases summed up in mg CO_2 Equation.

Treatment	N_20_E (mgm^{2}h^{-1})	CH_4_E (mgm^{2}h^{-1})	CO_2 (mgm^{2}h^{-1})	Total (mg CO_2 E)
Control	−1.07 ± 0.76	207.54 ± 119.81	174.80 ± 124.72	381.27 ± 124.72
Under	−0.18 ± 0.13	173.19 ± 60.41	208.81 ± 36.20	381.83 ± 69.86
Standard	1.30 ± 0.94	100.09 ± 158.50	248.29 ± 41.22	349.69 ± 170.77

Values are presented as mean ± standard error. The GWP of CH_4 and N_2O calculated using the IPCC GWP factors.

(Whiting and Chanton, 2001). The dry incidents experienced during sampling could have led to oxygen supply into the soil, enhancing the aeration, and thus increased CO_2 emissions. In rice paddies, apart from drainage, oxic conditions also occur at the soil-water interface and in the roots hence increasing CO_2 emissions to the atmosphere (Boateng et al., 2017). A study done by Cheng-Fang et al. (2012) showed no significant effect of N fertilizer application on cumulative CO_2 emissions. These results are consistent with the findings of this study where CO_2 emissions within the plots treated with different fertilization scenarios did not differ significantly. However, variable results have been reported from different studies where (Xiao et al., 2005; Iqbal et al., 2009) reported increased CO_2 emissions with use of N fertilizer from rice paddy farms whereas (Burton et al., 2004) recorded a decrease in CO_2 emissions with use of N fertilizer. Long term studies are necessary to improve the understanding of the effect of fertilizer application on carbon stocks and CO_2 emissions in rice paddies.

Nitrogen fertilizer application affected the nitrogen stocks and therefore a notable difference in N_2O emission from the three treatments. Emission of N_2O is influenced by the availability of nitrogen species (NH_4-N and NO_3-N) in the soil since they are required by microbes for nitrification and denitrification processes (Cowan et al., 2015). Bin-feng et al. (2016) reported that N_2O emissions became progressively greater as the quantities of N fertilizer increased. The study noted that N inputs in the range of 52.5–300 kg N ha^{-1} per season caused a significant increment (average 145%) in N_2O emissions. When fertilizer is applied into the soil, there is increased supply of nitrogen substrate for decomposers resulting to enhanced emission of N_2O (Chirinda et al., 2018). Linquist et al. (2012) meta-analysis study also reported that N_2O emissions increased significantly with increasing N fertilizer application rates, which is in agreement with the findings of this study.

Despite the observed differences in the emission levels of the three treatments, their net N_2O emissions were still very low. The low N_2O emissions could be attributed to other environmental factors like immobilization and retention of N fertilizer in soil (Fuhrmanna et al., 2018). The low N_2O fluxes could also be due to some of the nitrogen being–lost through leaching thus reducing amount of nitrogen substrate available for N_2O emissions. Bronson et al. (1997) in their study also observed negligible N_2O emissions during rice growing season when the soil is flooded. This is probably because the strictly anoxic conditions in the flooded paddies are suitable for denitrification and the major product of this process is nitrogen gas (N_2).

The greenhouse gases have varying residence time in the atmosphere and they all have different radiative force and thus different global warming potential GWP. The global warming potential of each gas is measured over a certain period of time using CO_2 as the reference gas. Over a span of 100 years, the GWP for CO_2, CH_4, and N_2O have been found to be 1, 25, and 298, respectively (Solomon et al., 2007). To evaluate the overall effect of GHG production in this study, the GWPs was applied to the fluxes measured and then carbon dioxide equivalent (CO_2 Eq) summed up. However, the effect of the three treatments on the overall GWP was not significant. This could be probably because of the short duration of the study and the similar weather conditions experienced in all the treatment plots. Fertilizer application had no effect on the net GWP. This is in contrast with the study by Bin-feng et al. (2016) which noted that response of GWP to N addition was 3-10 folds greater for fertilization of 250–300 kg N ha^{-1} (266%) than for 50–250 kg N ha^{-1} (26 to 80%). Methane and nitrous oxide emissions from rice fields are however of great concern due to their radiative effects as well as GWP (IPCC, 1995).

Land use change is the major driver of loss of ecosystem services. Ecosystem services maybe lost or reclaimed through change in land use. Wetlands have various roles to human well-being including; provisioning (food, water, and raw materials, fuel), regulating (floods, climate change through carbon sequestration, and water purification), and cultural (aesthetic, spiritual, educational, and recreational) services (MEMR, 2012). Despite their critical role, wetlands are being degraded rapidly and they suffer the greatest transformations worldwide (Zorrilla-Miras et al., 2014). Globally, wetlands losses due to conversion to arable cropping have been the key drivers to degradation of wetlands and increased emission of greenhouse gases (Tangen et al., 2015). The major wetland function impacted by land use change is loss of ability to sequester carbon. Wetlands accumulate carbon in soil and their expansive canopy litter due to anaerobic conditions which results to slow decomposition rates of organic carbon (Batson et al., 2015). However, during land preparation and cultivation for planting rice, the soil organic matter is exposed to favorable decomposition conditions which enhances loss of soil carbon as CO_2. Use of different fertilizers (organic or inorganic) alter the chemical budget adds nutrients into the wetland and; as a result, impair the wetlands ability to purify water (nutrient sink). Cultural value of wetland is also lost when wetlands are cleared for agricultural use.

CONCLUSION

This study assessed soil organic carbon, soil nutrients stocks and greenhouse gas emissions under different treatments including: control (no fertilizer applied), under-fertilization (involved first and second topdressings fertilizer application only), and standard fertilization (involved basal, first and second fertilizer application). The various fertilization regimes did not significantly affect the soil nitrogen species (ammonium and nitrate), total nitrogen and soil organic carbon stocks. Although the fertilizer application regime did not affect the amount of available ammonium and nitrate, there was a significantly higher N_2O emission under standard fertilization compared to no fertilizer application. Fertilizer application regime however, had no effect on CH_4 and CO_2 emissions in the short time of the study. From this study, even though the effect of the three fertilizer application scenarios was not significant, we can conclude that cultivation and land preparation for planting rice increased the loss of organic carbon in the form of CO_2 and therefore the ability of the Anyiko wetland to store carbon was reduced. Use of nitrogenous fertilizer also led to impairment the of climate change regulatory function of the Anyiko wetland. Our findings suggest that the cumulative effects of such changes in the wetland land use may have negative implications on the ecosystem climate change regulating services.

LIMITATIONS OF THE STUDY

The study was conducted during rice growing period and therefore, only provides limited information on temporal variations of the GHG emissions in the rice fields. A year-round study would provide adequate information on emission levels before planting (when the land is bear), during rice growth and after planting.

The study was only conducted in the rice paddies. A concurrent study on the nutrient and organic carbon stocks, and GHG emissions in the natural wetland would provide useful information on the climate regulating ecosystem service of the wetland.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

CO designed the study, fabricated the gas chambers, collected the samples, analyzed the data, and wrote the manuscript. NK and JK gave guidance on the study design and assisted on the manuscript write up. RO gave guidance on gas chambers fabrication, study design and assisted on the manuscript write up. All authors contributed to the article and approved the submitted version.

FUNDING

This research was funded by Rotary Club of Vienna.

ACKNOWLEDGMENTS

Our gratitude goes to the LWM programme, Department of Biological Sciences and Department of Soil Science Egerton University and International Livestock Research Institute (ILRI), Mazingira Centre, for giving us lab space and equipment to carry out our research work. We appreciate the support from Dr. Lutz Merbold and Mr. Paul Mutuo of ILRI, Mazingira Centre. We are also grateful to Mr. Erick Owino of Egerton University for field assistance.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 31 July 2020
doi: 10.3389/fenvs.2020.00122

Sediment and Nutrient Retention Capacity of Natural Riverine Wetlands in Southwest Ethiopia

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Although wetlands in temperate regions have been studied for their pollutant remediation potential, the sediment and nutrient retention capacity of natural wetlands in tropical environments remains understudied. In this study, a mass balance approach was used to estimate the amount of sediment and nutrients retained at 40 different study sites located in four natural riverine wetlands in Southwest Ethiopia. Awetu and Boye wetlands retained a substantial amount of total suspended solids (TSS) and nutrients whereas Kofe and Kito wetlands had a net release. Overall, the amount of TSS retained by the four wetlands was estimated to be 6266.5 kg/ha/day. On the other hand, the net retention of Total Organic Nitrogen (TON) and Total Phosphorous (TP) was estimated to be 37.6 kg/ha/day and 40.9 kg/ha/day, respectively. A stepwise multiple regression analysis revealed that anthropogenic activities such as farming, grazing, waste dumping and clay mining were the main variables that negatively affected the retention of TSS and nutrients. Farming alone explained 58% of the variation in TSS retention and cattle grazing explained 25% of the variation in TON retention. Therefore, watershed management interventions considering the mitigation of anthropogenic activities could be considered to reduce sediment and nutrient input and release.

Keywords: anthropogenic disturbance, multiple regression, nutrients, retention capacity, riverine wetland, total suspended solids

OPEN ACCESS

Edited by:
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Joris Eekhout,
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Specialty section:
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

Received: *28 February 2020*
Accepted: *06 July 2020*
Published: *31 July 2020*

Citation:
Mereta ST, De Meester L, Lemmens P, Legesse W, Goethals PLM and Boets P (2020) Sediment and Nutrient Retention Capacity of Natural Riverine Wetlands in Southwest Ethiopia. Front. Environ. Sci. 8:122. doi: 10.3389/fenvs.2020.00122

INTRODUCTION

Wetlands provide many ecosystem services such as habitat for plants and animals including endangered species, products (such as fish, reed, timber, fuel, wood, and medicines), mitigation of floods, recharging of aquifers and an improvement in water quality (Millennium Ecosystem Assessment, 2005; Mateos et al., 2009). Water quality functions of wetlands are a composite of many different biogeochemical and mechanical processes, which act collectively to alter and usually improve the quality of surface waters (Mateos et al., 2009). Biogeochemical processes that occur within wetlands can effectively remove a variety of pollutants from the water column (Knox et al., 2008). These processes include microbial transformation to gaseous forms, plant uptake of nutrients, and microbial degradation of pesticides and other organic compounds and sedimentation (Woltemade, 2000; Jordan et al., 2003; Fisher and Acreman, 2004; Knox et al., 2008).

Wetlands can serve both as sink and sources for contaminants (Kadlec and Reddy, 2001). The pollutant retention capacity depends on the structure and functioning of the wetland, and can also be influenced by hydrologic and temperature regimes (Kadlec and Reddy, 2001; Kadlec, 2009). In tropical climates, humidity is high year-round, although there may be a distinct wet and dry season. In addition, ambient temperature does not show substantial temporal variation as in temperate climates, which can impact plant growth and hence also pollutant retention capacity.

Wetland ecosystems are effective sediment traps, generally retaining more suspended sediments than they release (Christopher and David, 2004; Sileshi et al., 2020). Sediment deposition in wetlands is an important mechanism to improve water quality as sediments retain nutrients and toxic substances through sorption processes (Cooper et al., 2000; Noe and Hupp, 2009). The retention of suspended solids in wetlands is controlled by particle size, hydrologic regimes, flow velocity, wetland morphometry and water residence time (Verstraeten et al., 2006). Plants in wetlands can increase the hydraulic resistance and decrease flow velocity, which enhances settling and deposition of suspended solids (Paudel et al., 2013). In addition, aquatic plants retain nutrients through vegetative uptake, create root channels that increase infiltration capacity, provide a large surface area for microbial growth, and transport oxygen to anaerobic layers (Schoonover et al., 2005).

Wetlands can act as sinks and converters of nitrogenous compounds by various mechanisms (Keenan and Lowe, 2001; Jordan et al., 2003). These mechanisms include denitrification, assimilation, and retention by vegetation, converting nitrates to ammonia and organic nitrogen (Jordan et al., 2003). Vegetation plays a crucial role as it affects denitrification and nitrification by influencing oxygen concentrations in wetland substrates within the rhizosphere (Paudel et al., 2013). Phosphorous retention by wetlands is driven by a combination of chemical, biological and physical processes (Reddy et al., 1999). These processes are regulated by vegetation, periphyton, plant litter and detritus accumulation, flow velocity, water depth, hydraulic retention time and hydrologic fluctuations (Jordan et al., 2003; McJannet, 2007).

The loss and degradation of wetlands is a world-wide phenomenon (Russi et al., 2013) and undermines their pollutant mitigation potential (e.g., Mironga, 2005). The major direct drivers of wetland degradation and wetland loss include intensive agriculture, discharge of untreated wastewater, overgrazing and deforestation (Millennium Ecosystem Assessment, 2005). The use of fertilizers to enhance agricultural production often leads to eutrophication of surface waters (Crumpton, 2001; Zhenlou et al., 2002). Moreover, intense agriculture and deforestation can cause runoff and landslides that both increase the concentration of sediments in rivers and wetlands (Broothaerts et al., 2012). In Ethiopia, the occurrences of landslides are facilitated by steep slopes, extreme rainfall events, high human population pressure and severe deforestation (Broothaerts et al., 2012). The resulting increase in sediment loads results in enhanced sedimentation in reservoirs and dams, which reduces their water storage capacity (Devi et al., 2008; Adwubi et al., 2009). Assessments estimated that the volume of the reservoir of the Gilgel Gibe I hydroelectric dam, situated in southwest Ethiopia, will be reduced by half within 12 years (Devi et al., 2008). Although the reservoir was expected to serve for at least 70 years, there is a risk that the reservoir will be completely filled with sediments and characterized by highly eutrophic conditions 24 years after its construction (Devi et al., 2008).

Although constructed wetlands in temperate regions have been extensively studied and are generally considered as effective systems for sediment and nutrient retention, the retention efficiency of natural wetlands in tropical environments is considerably less investigated (McJannet, 2007). The objective of this study was to determine the total suspend solids (TSS) and nutrient retention capacity of natural riverine wetlands in Southwest Ethiopia, and to identify the effect of anthropogenic stressors on this retention capacity. Such information provides pivotal information for the development of sustainable wetland conservation programs in Ethiopia, where wetlands are important biodiversity hotspots and natural resources for food security and rural livelihood, but at the same time are highly threatened by unregulated exploitation and a lack of management.

MATERIALS AND METHODS

Study Area

This study was conducted in the Awetu sub-catchment, part of the Gilgel Gibe I watershed, situated in Southwest Ethiopia and lying between latitudes 7°37′N and 7°53′N and longitudes 36°46′E and 37°43′E (**Figure 1**). The total area of the sub-catchment is about 500 km^2. Elevation of this sub-catchment area ranges between 1,700 and 2,610 ma.s.l. The mean annual temperature ranges between 15°C and 22°C, and the mean annual precipitation ranges between 1500 mm and 2300 mm, with maximum rainfall from June till early September and minimum precipitation between December and January (National Meteorological Agency, 2013). Four riverine wetlands: Awetu (AW), Boye (BO), Kito (Kt) and Kofe (Kf) were investigated in this study. These wetlands varying in size ranging from 12 to 110 hectares. Streams flowing through these wetlands had an estimated mean discharge of 10.55 m^3/sec, contributed to about 25% to the flow of the Gilgel Gibe River, one of the tributary of the Gilgel Gibe I reservoir situated 60 km downstream of the studied wetlands. The major threats to these wetlands include disposal of domestic sewage, drainage, farming, clay mining, removal of riparian vegetation and intensive livestock grazing. Awetu, Boye and some parts of Kito wetlands received untreated wastewater generated by the more than 200,000 inhabitants of Jimma town. Clay mining, drainage, Eucalyptus plantation vegetation clearance and filling were the common practices in Kofe and Kito wetlands (**Table 1**).

Riverine wetlands in Southwest Ethiopia have been extensively modified during the last years by human activities (Mereta et al., 2013; De Troyer et al., 2016; Chawaka et al., 2018). The major threats from human activities in and around these wetlands

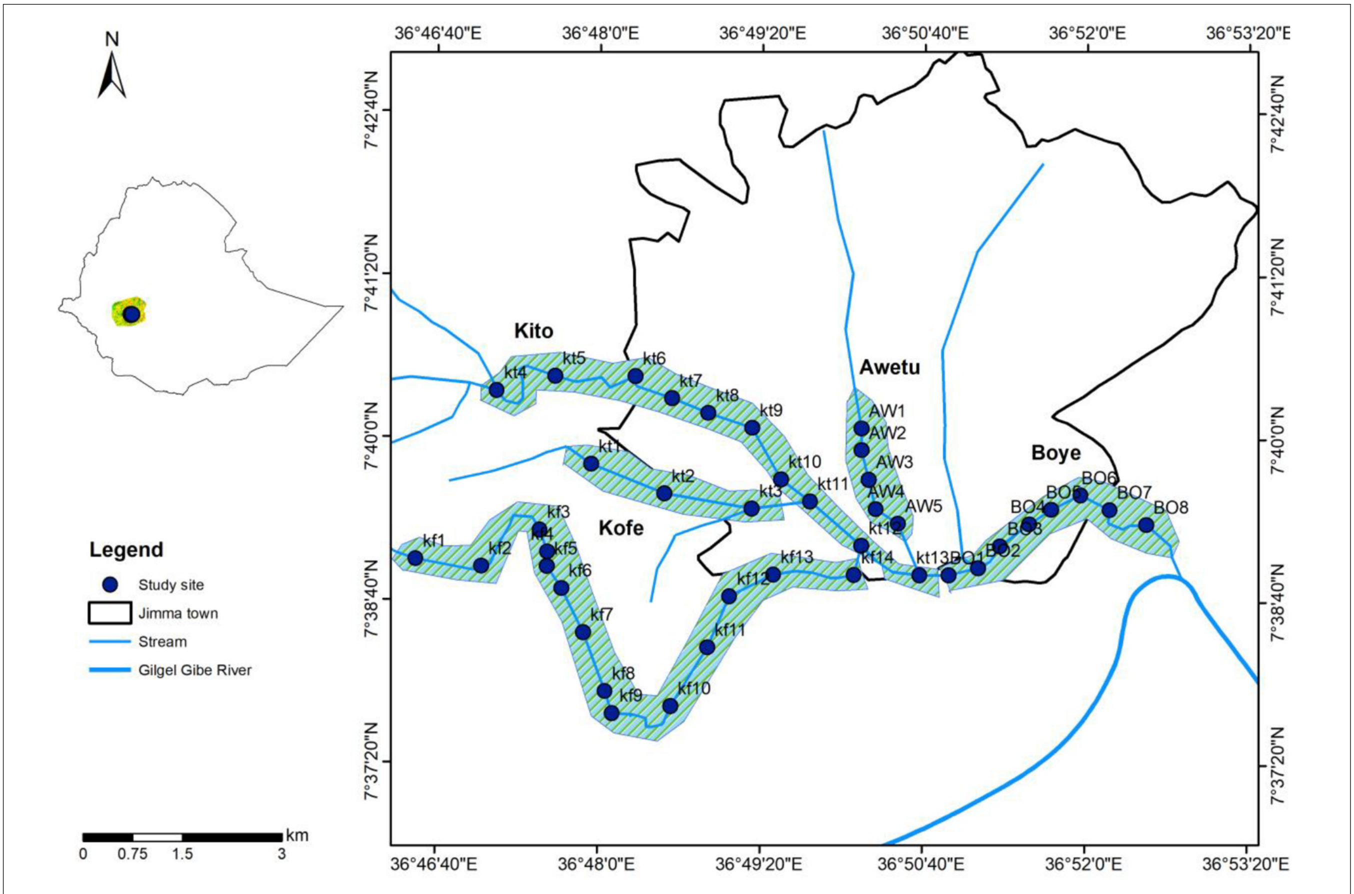

FIGURE 1 | Map of wetland sampling sites in the neighborhoods of Jimma, Southwest Ethiopia (Kf = Kofe, Kt = Kito, AW = Awetu, BO = Boye).

include disposal of domestic sewage, drainage, farming, clay mining, removal of riparian vegetation and intensive livestock grazing (Mereta et al., 2013). In addition, river incisions and back erosions as a result of heavy rainfall, steep slopes and deforestation have contributed to landslides in the catchment (Broothaerts et al., 2012). This has led to extensive erosion from the upland areas and to increases in the sediment load in the receiving rivers and siltation problems in the Gilgel Gibe I reservoir, which may interfere with its hydroelectric generating capacity and the provision of other ecosystem services.

Data Collection

A total of 40 sites were selected in four wetlands along a gradient of anthropogenic impacts including both nearly non-impacted and heavily disturbed sites (e.g., presence of point source pollution, eutrophication, hydrological modification, etc.), similar to a previous study conducted by Mereta et al. (2013). The number of sampling sites was evenly distributed among the wetlands depending on their size (**Figure 1**), with the smallest wetlands having a lower number of sampling sites. Sites up- and downstream of river confluences were included, since this allowed us to assess the impact of the confluence on the receiving wetland or stream. Wetland sampling sites were monitored twice a year: once during the dry (February and March) and once during the wet season (i.e., after the end of rainy season October to November) in 2011. Awetu wetland was sampled only during the wet season of 2011. In total, 75 samples were collected. Geographic coordinate readings were recorded for all sampling sites using a hand-held global positioning system unit (GPS) (Garmin GPS 60, Garmin international Inc., and Olathe, Kansas, United States). Coordinate readings were integrated into a GIS database using Arc MAP 10 GIS software. All digital data in the GIS were displayed in the World Geodetic System (WGS) 1984 Coordinate system.

Habitat Sampling and Classification

Habitat characteristics of the surrounding area were assessed at each sampling station using the USEPA wetland habitat assessment protocol (Baldwin et al., 2005). The degree of hydrological modifications (drainage, ditching and filling), habitat alteration (tree removal, tree plantation and grazing) and land use patterns such as waste dumping, clay mining, and farming were assessed during sampling. Draining refer to water-level drawdown. It is a very common practice in the study area mainly for the cultivation of the dry season maize (Zea mays). Filling refers to placement of materials in the wetlands for conversion to other land-uses such as cultivation, house construction and so on.

TABLE 1 | Characteristics of the study wetlands located in the Gilgel Gibe I watershed, southwest Ethiopia.

Name of wetland	Number of sites monitored	Area (hectare)	Discharge (m^3/sec)	Human disturbance
Awetu	5	12	1.2 (0.8–1.6)	Waste dumping, Drainage, Farming, Grazing, Water abstraction
Boye	8	90 (85–95)	5.2 (2.4–8.0)	Waste dumping, Drainage, Farming, Grazing, Water abstraction
Kito	13	93 (90–96)	3.75 (2.55–4.95)	Waste dumping, Drainage, Farming, Grazing, Water abstraction, Eucalyptus plantation, Clay mining, Filling
Kofe	14	100 (90–110)	0.4 (0.2–0.6)	Vegetation clearance, Eucalyptus plantation, Drainage, Farming, Grazing, Clay mining, Filling

Mean values and range.

Land use, habitat alteration and hydrological modifications were quantified based on their intensity in the studied wetlands according to Mereta et al. (2013). A score of 1 was assigned to no or minimal disturbance, 2 to moderate and 3 to high disturbance (**Supplementary Material S1**). The final disturbance score was then computed by summing nine disturbance types generating a disturbance score ranging from 9 to 27. This score was then divided into five classes: 9–11 = very low, 12–15 = low, 16–19 = moderate, 20–23 = high, and 24–27 = very high.

Climate data of the year 2011 was used for this study. Daily weather data of the surrounding area was collected from Jimma meteorological station situated near the study wetlands, about 6 km from the farthest wetland site.

Water Sampling and Analysis

Water samples were taken 20 cm below the surface in the water column to avoid scum. A 500 ml sample of unfiltered water was collected for analysis of total organic nitrogen (TON) and total phosphorous (TP). Unfiltered water samples were kept cool and dark during transportation to the laboratory of Environmental Health Science and Technology, Jimma University, for further analysis. Total phosphorus samples were first digested in a block digester using ammonium persulfate and a sulfuric acid reagent (APHA et al., 1995). Total phosphorous was analyzed using the stannous chloride method (APHA et al., 1995). Samples of TON were also digested and measured with photometric kits (Hach Lange) using a Hach DR5000 spectrophotometer.

For total suspended solid (TSS) determination, a known volume of water was filtered through a pre-dried (105°C; 12 h) and pre-weighed Whatman Glass Microfiber filter (GF/C-filters, diameter 47 mm and pore size 1.2 μm). After sampling, the filters were dried in an oven at 105°C for 12 h, cooled in desiccators to balance temperature, and weighed. The TSS concentration was calculated as the difference between the weight of the filter plus the dried residue and the weight of the filter; the value obtained from this difference was divided by the sampled volume. The dried residue was combusted at 550°C for 20 min in a muffle furnace to determine the volatile suspended solids (VSS) (organic fraction). The concentration of volatile suspended solids was calculated as the difference between the weight of the recipient plus the weight of the dried residue before combustion and the weight of the recipient and this difference was divided by the sampled volume. The concentration of fixed suspended solids was calculated as the difference between the total suspended solids and the volatile suspended solids.

Measuring Flow Velocity and Discharge

The volume of water inflow and outflow of the wetland was calculated by multiplying the area of water in the channel cross section by the average flow velocity of the water in that cross section. First, the channel cross section was divided in 5 to 10 subsections depending on the channel size. In each subsection, the area was calculated by measuring the width and depth of the subsection and by multiplying these values. Average flow velocity was computed from three repeated measurement at each cross section using a flow meter (BFM001channel flow meter, Valeport, United Kingdom). The discharge in each subsection was calculated by multiplying the subsection area by the measured average flow velocity. The total discharge was then calculated by summing the discharge of each subsection.

$$\begin{aligned}\text{Total discharge } &= (\text{Area}_1 * \text{Velocity}_1) + (\text{Area}_2 * \text{Velocity}_2) \\ &\quad + \ldots + (\text{Area}_x * \text{Velocity}_{xx}) \end{aligned} \tag{1}$$

Loading and Flux Calculation

A nutrient and sediment loading rate of the wetland was calculated by multiplying the measured concentrations of nutrients and sediments, respectively, by the instantaneous discharge. The loading rates were corrected for water loss through evaporation and water input from precipitation.

$$\begin{aligned}&\text{Loading (kg/day)} \\ &\quad = \text{Concentration (kg/m}^3) * \text{Discharge (m}^3\text{/day)}\end{aligned} \tag{2}$$

Fluxes (surface loadings) were then calculated by dividing loading rate by wetland surface area (hectare).

$$Flux(kg/ha/day) = \frac{Loading\ (kg/day)}{Area\ (ha)} \tag{3}$$

Retention rates are typically calculated by subtracting outputs from inputs. This yields positive values when pollutants are retained in the wetland and negative values when pollutants are released. Hence, negative retention refers to release. In this case wetlands act as a source of pollutants.

Data Analysis

Nutrients and TSS data were log transformed [log(x + 1)] prior to analysis to meet normality assumptions. A Principal

Component Analysis (PCA) was used to reduce the dimensions of human disturbance by creating a latent variable based on the PCA coordinates. Principal components were computed using the Oblimin rotation method with a Kaiser Normalization. The components were extracted based on eigenvalues greater than 1. Afterward, a stepwise multiple regression analysis was conducted by regressing the component scores computed by the PCA in order to identify which set of disturbance factors best explained the variation in nutrient and TSS retention. The concentration of total suspended solids was the response variable, whereas the habitat disturbances were the explaining variables. In case of nutrients (TON and TP), the response variable was composed of all individual nutrient measurements, whereas the habitat disturbances were the explanatory variables. We used a two-way ANOVA to select the most parsimonious model. The goodness of fit of each regression model for the data was evaluated based on the F-test and adjusted R-squared value.

Box- and Whisker plots were used to visualize the retention of TSS and nutrients at different levels of disturbance in the different wetlands. A non-parametric Kruskal-Wallis test was used to determine whether there were significant differences in the retention of TSS and nutrient concentrations between different levels of disturbance within the wetlands. We used a Wilcoxon rank-sum test to explore differences in retention between the dry and wet season.

Principal Component Analysis (PCA) and multiple regression were performed using Spss Inc (2007) (version 16) (SPSS Inc., Chicago, IL), whereas ANOVA analyses were done with STATISTICA 7.0 (Statsoft Inc, 2004). *P*-values < 0.05 were considered significant.

RESULTS

Total Suspended Solids Concentration and Retention

From Kf1 to Kf14, the TSS concentration increased from 15 mg/l to 26 mg/l during the wet season and decreased from 37 mg/l to 26 mg/l during the dry season (**Figures 2A,B**). In kofe wetland the TSS concentration ranges from 4.5 mg/l to 39 mg/l. The net TSS release of Kofe wetland was 221 and 94 kg/ha/day for the wet and dry season, respectively (**Table 2**). The ratio between volatile suspended solids (VSS) and total suspended solids (TSS) in this wetland ranged from 0.5 to 0.6. The net TSS release during the wet season was significantly higher than during the dry season ($p = 0.002$).

The highest concentration of TSS was measured at Kt1, 122 mg/l during wet season and at kt5, 104 mg/l during the dry season (**Figures 2C,D**). Whereas the net TSS release for Kito wetland was 89 and 25 kg/ha/day for the wet and dry season, respectively (**Table 2**).The ratio between volatile suspended solids (VSS) and total suspended solids (TSS) in this wetland ranged from 0.5 to 0.7. The net release of TSS was significantly higher during the wet season than during the dry season ($p = 0.002$).

The highest concentration of TSS was recorded in the first upstream site location (AW1) 198 mg/l (**Figure 2E**). The net TSS retention in Awetu wetland was 6371 kg/ha/day. Kito stream, having an average flow rate of 3.75 m^3/s and an average TSS concentration of 8 mg/l, joins the outflow of Awetu below AW5 and flows through Boye wetland. The first upstream sampling point of Boye wetland (BO1) had a measured TSS concentration of 16 mg/l. The highest concentration of TSS (41 mg/l) was measured at BO4, after the entrance of Becho-Bore stream having a flow rate of 0.5 m^3/s and a TSS concentration of 88 mg/l. The net TSS retention in Boye wetland was 112 and 108 kg/ha/day during wet and dry season, respectively (**Table 2**). The ratio between volatile suspended solids (VSS) and total suspended solids (TSS) in this wetland ranged from 0.7 to 0.8.

Nutrient Concentration and Retention

The highest concentration of Total Organic Nitrogen (TON) (5.64 mg/l), was measured at Kf8 during the dry season (**Figures 3A,B**). The net release of TON in Kofe wetland was 2.8 kg/ha/day and 2.3 kg/ha/day for wet and dry season, respectively (**Table 2**). Likewise, the highest concentration of Total phosphorous (0.46 mg/l) was recorded at Kf8 during the dry season (**Figures 4A,B**). The net release of TP in Kofe wetland was 0.27 kg/ha/day and 0.07 kg/ha/day for wet and dry season, respectively. The net input and release of TP was significantly higher during the wet season than during the dry season ($p = 0.02$) (**Table 1**).

The highest concentration of TON (2.8 mg/l) was measured at Kt8 during the dry season where as the lowest concentration (0.03 mg/l) was recorded at Kt3 during the dry season (**Figures 3C,D**). The net release of TON in Kito wetland was 4.7 kg/ha/day and 3.8 kg/ha/day for wet and dry season, respectively. On the other hand, the highest concentration of TP was recorded at Kt8 (0.69 mg/l) during the dry season (**Figures 4C,D**). The net release of TP in Kito wetland was 4.1 kg/ha/day and 3.8 kg/ha/day for wet and dry season, respectively. There was no statistically significant difference in retention of TON between the dry and wet season ($p = 0.08$) (**Table 2**).

In Awetu wetland, the highest concentration of TON (1.28 mg/l) was measured at AW2, whereas the lowest concentration was measured at AW5 (0.97 mg/l) (**Figure 3E**). The net retention of TON in Awetu wetland was 18.3 kg/ha/day. On the other hand, highest concentration of TON in Boye wetland recorded at Boye 4 (2.23 mg/l). The net retention of TON in Boye wetland was estimated to be 27.6 kg/ha/day and 24.54 kg/ha/day for the wet and dry season, respectively. The net retention of TP in Awetu wetland was estimated to be 41 kg/ha/day whereas; Boye wetland had a net TP retention of 4.11 kg/ha/day and 3.8 kg/ha/day for the wet and dry season, respectively.

Impact of Disturbance on TSS Retention and Nutrient Retention

The first two PCA axes explained 73% of the total variation in human disturbance data. The factor loadings for the different variables are shown in **Supplementary Material S2**. The disturbance types that contributed most to the variation in PCA1 were: draining, farming, vegetation clearance, clay

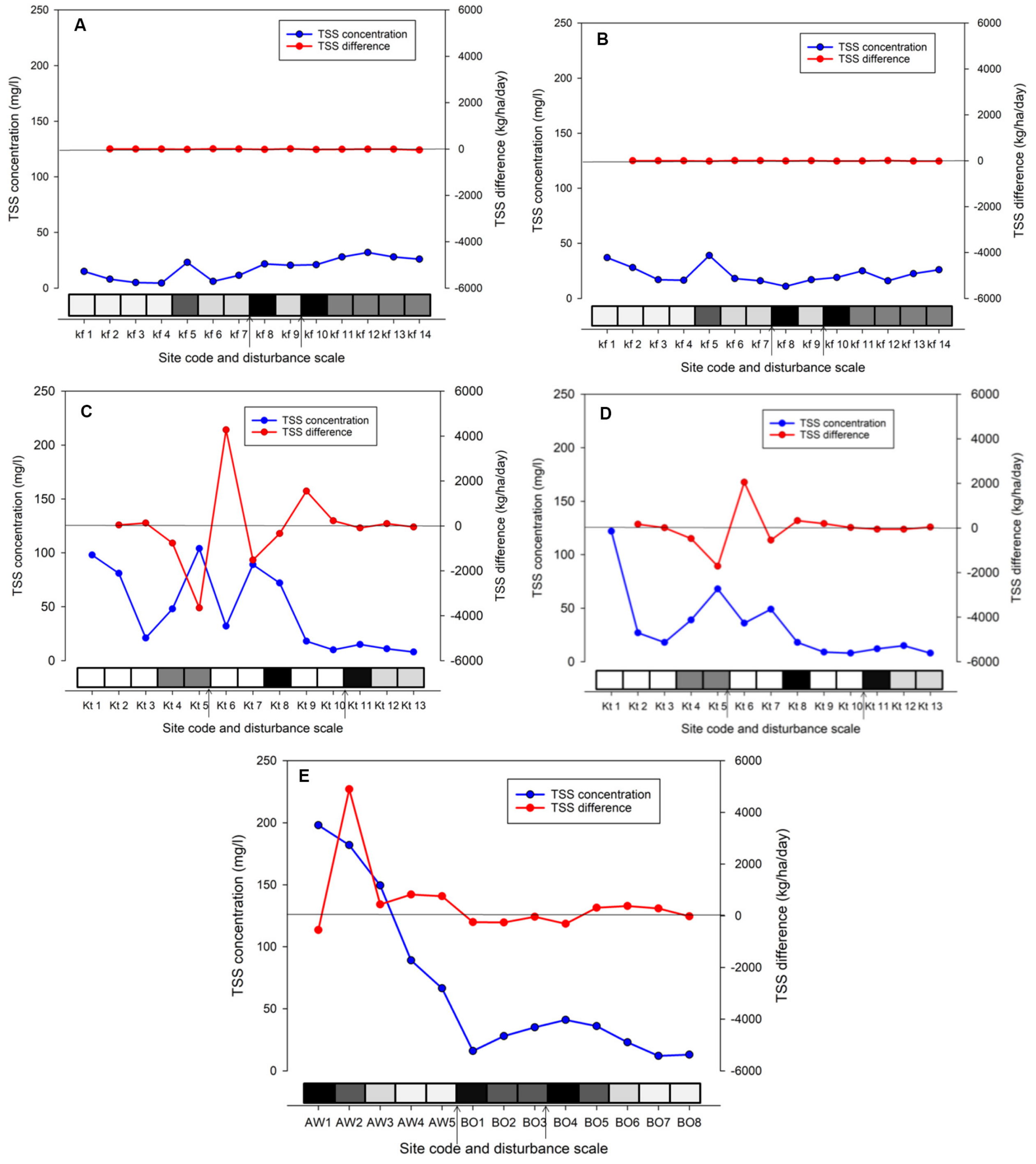

FIGURE 2 | Total Suspended Solids (TSS) concentration and difference in Kofe **(A)**, Kito **(C)** and Awetu-Boye **(E)** wetlands during wet season and Kofe **(B)** and Kito **(D)** during the dry season. Disturbance condition along the wetland ranged from very low (white) to very high (black). A black arrow indicates a site where a tributary enters into the main stream.

mining, grazing, filling and waste dumping. The second axis was mainly related to plantation and water abstraction. Among the nine disturbance factors, draining and vegetation clearance were significantly correlated with farming and had a variance inflation factor of 11 and 6, respectively. Accordingly, these two variables were excluded from the final analysis. Out of the seven remaining variables, only four disturbance types contributed to the final linear regression model. Filling, plantation and abstraction had no significant contribution to the regression model and were therefore removed. This model explained 73% of the variation

TABLE 2 | Sediment and nutrients retention/release capacity of wetlands in the Gilgel Gibe I watershed.

Variables	Awetu		Boye		Kito		Kofe		*P*-value
	Wet season	Dry season	Wet season	Dry season	Wet season	Dry season	Wet season	Dry season	
TSS (mg/l)	137 ± 51	Na	65.5 ± 6.8	63 ± 12	37 ± 21	33 ± 12	17.9 ± 9.5	22 ± 8.2	**0.002**
FS (mg/l)	41 ± 13	Na	18 ± 2.8	21 ± 3.2	9 ± 6.4	7 ± 5.4	5 ± 3	5 ± 3	**0.002**
VS (mg/l)	96 ± 34	Na	46 ± 2.8	42 ± 3.2	28 ± 13	17 ± 11	9.2 ± 6.4	13.2 ± 7.2	**0.002**
TON (mg/l)	1.15 ± 0.11	Na	1.46 ± 0.4	0.96 ± 0.2	0.99 ± 0.45	0.4 ± 0.38	0.74 ± 1.3	0.7 ± 1.7	**0.04**
TP (mg/l)	0.83 ± 0.4	Na	0.1 ± 0.06	0.2 ± 0.08	0.11 ± 0.15	0.2 ± 0.18	0.6 ± 0.32	0.7 ± 0.38	**0.02**
TSS retention (kg/ha/day)	6371	Na	112	108	−89	−25	−221	−94	**0.002**
TON retention (kg/ha/day)	18.3	Na	27.6	24.54	−4.7	−3.8	−2.8	−2.3	**0.08**
TP retention/release kg/ha/day)	41	Na	4.11	3.8	−4.1	−3.8	−0.27	−0.07	**0.02**

Mean values and standard deviation. P-values related to significant differences between seasons are indicated in bold. A negative retention was considered as release. TSS = Total suspended Solids; FS = fixed Solids; VSS = Volatile Suspended Solids; TON = Total Organic Nitrogen, TP = Total Phosphorous.

in TSS retention ($N = 75$; $R^2 = 0.73$; $p < 0.001$). The retained variables for the final model were: farming, waste dumping, clay mining and grazing. Farming alone explained 58% of the variation ($R^2 = 0.58$) (**Supplementary Material S2**). The Kruskal-Wallis test indicated that sites with low degree of disturbance had a significantly higher TSS retention than moderately to highly disturbed sites ($p < 0.05$) (**Figures 5A–C**).

The stepwise multiple regression model was able to explain 28% of the variation in TON retention data ($N = 75$, $R^2 = 0.28$, $p < 0.001$). The remaining 72% of the variation could be unmeasured wetland specific conditions which might contribute to the retention/release of nutrients. The retained variables for the final model were: grazing, waste dumping and farming. Grazing alone explained 25% of the variation ($R^2 = 0.25$) (**Supplementary Material S3**). The Kruskal-Wallis test indicated that there was a significant difference in TON retention among different classes of disturbance $p < 0.001$ (**Figures 5D–F**).

DISCUSSION

Overall, the TSS and nutrients retention capacity of wetlands was largely governed by the quality of water inflow and human disturbance. This study demonstrates that Awetu and Boye wetlands retained a substantial amount of total suspended solids (TSS) and nutrients, although the outflow concentrations were still higher than the other two wetlands. The higher loading rate of TSS and nutrients to Awetu and Boye wetlands might be attributed the discharge of untreated wastewater and solid wastes generated by more than 200,000 inhabitants of Jimma town into the tributaries of Awetu and Boye wetlands (Haddis et al., 2014). Indeed, a study on constructed wetlands has shown that higher mass loading rates generally result in higher sediment and nutrient retention rates (Redmond et al., 2014).

On the other hand, Kofe and Kito wetlands had relatively good water quality at the upstream sampling locations. However, water quality deteriorates as it flows in the downstream locations mainly due to human induced activities such as clay mining, eucalyptus plantation, farming and grazing. As a result, Kofe and Kito wetlands act as sources of TSS and nutrients (negative retention rate). The release of TSS and nutrients was higher during the wet season than the dry season. This might be the results of seasonality in rainfall that can lead to shifts in hydrologic connectivity between constituent water sources and wetland tributaries. Earlier studies have shown that changes in frequency, timing and intensity of rainfall events do not only alter runoff patterns, but can also affect subsequent pollutant loading (Borris et al., 2014). The total annual precipitation at the study area was calculated to be 1560 mm, two-third of which precipitated during the wet season (between June to September) (**Supplementary Material S5**). This might contribute to the high release of sediment and nutrients during the wet season.

Despite the high levels of TSS recorded in some wetlands, our results show that 50 to 80% of the TSS consisted of Volatile Suspended Solids (VSS), indicating that a large fraction of the TSS is organic and can be degraded by biological activity. The amount of TSS retained by the investigated wetlands is estimated to be 1848.6 ton per day. Out of which, 35% (647 ton/day) were fixed solids which can be accumulated in the downstream locations including the floodplains and Gilgel Gibe I reservoir. Therefore, the study wetlands play a role in the retention of about 236,161 tons of sediment per annum which potentially occupies 157,441 m^3 space per annum. This volume is equivalent to 0.02% of the Gilgel Gibe I reservoir active capacity. The active capacity of Gilgel Gibe I reservoir is estimated to be 717,000,000 m^3.

In this study, large variation in TSS and nutrient retention capacity was observed between sampling sites within wetlands. TSS and nutrient retention were strongly and negatively impacted by the degree of habitat disturbance. Habitat disturbances, particularly the conversion of riparian wetlands into cultivated land, livestock grazing, clay mining and waste dumping were found to contribute to the release of TSS and the increase in nutrients in the wetlands. The stepwise regression analysis revealed that farming activities are highly and negatively related to TSS retention. Drainage and vegetation clearing of wetlands for agricultural production results in increased degradation and reduced retention capacity. Similarly, Knox et al. (2008) reported that wetlands drained for agricultural use were characterized by lower retention rates and higher export of nutrients and sediments compared to natural reference wetlands, a phenomenon that was also observed in our study.

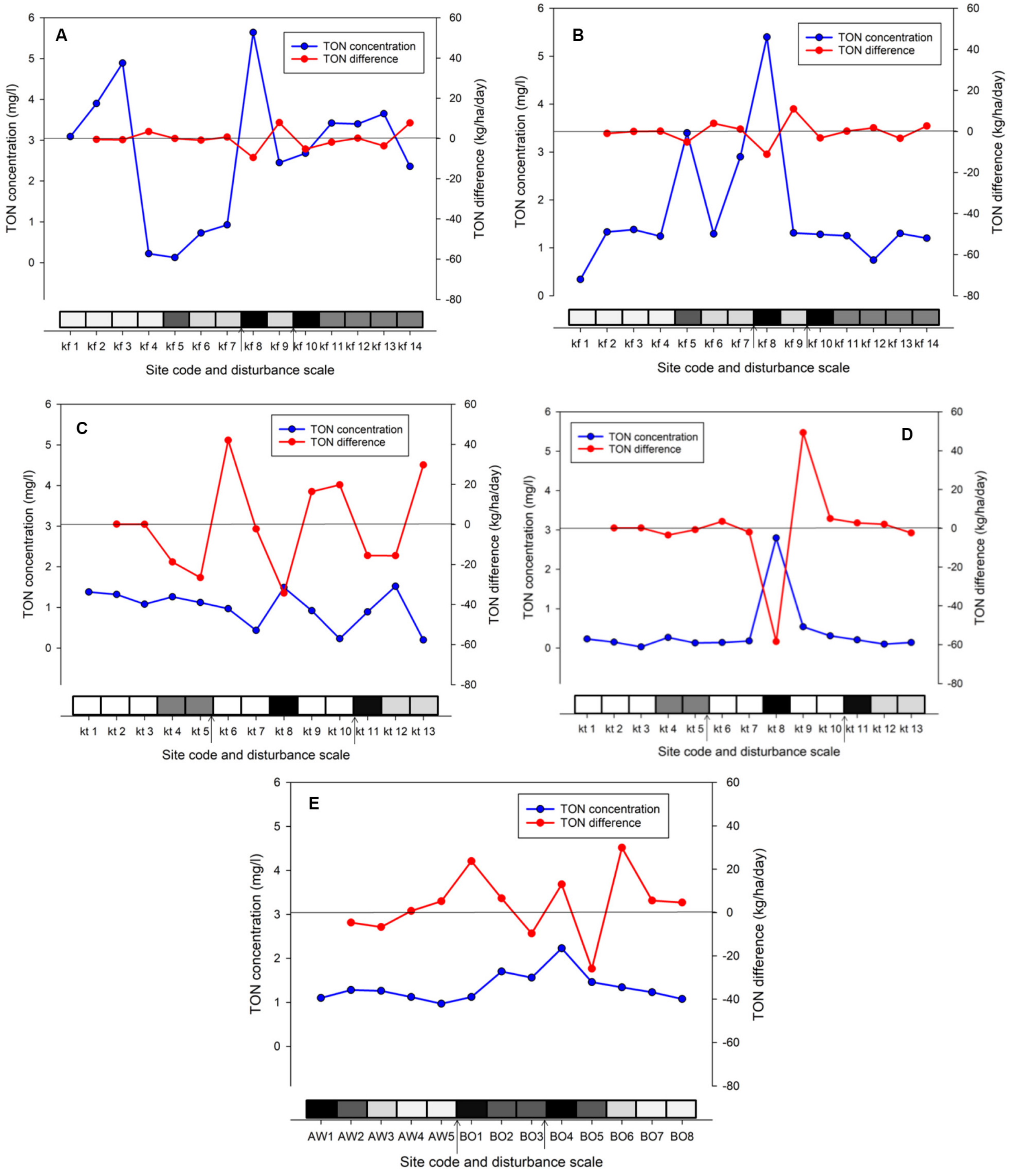

FIGURE 3 | Total Organic Nitrogen (TON) concentration and difference in Kofe **(A)**, Kito **(C)** and Awetu-Boye **(E)** wetlands during wet season and Kofe **(B)** and Kito **(D)** during the dry season. Disturbance condition along the wetland ranged from very low (white) to very high (black). A black arrow indicates a site where a tributary enters into the main stream.

Our results indicate that grazing explains 25% of the variation in nutrient retention. Grazing alters the hydrology and the drainage pathways at a site by compacting the topsoil, which in turn decreases the infiltration capacity of the soil (Gathumbi et al., 2004; Pietola et al., 2005) and, consequently, leads to an increase in the release of nutrients and sediments by erosion (Kurz et al., 2005). In addition, grazing may lead to alteration in wetland plant community composition and

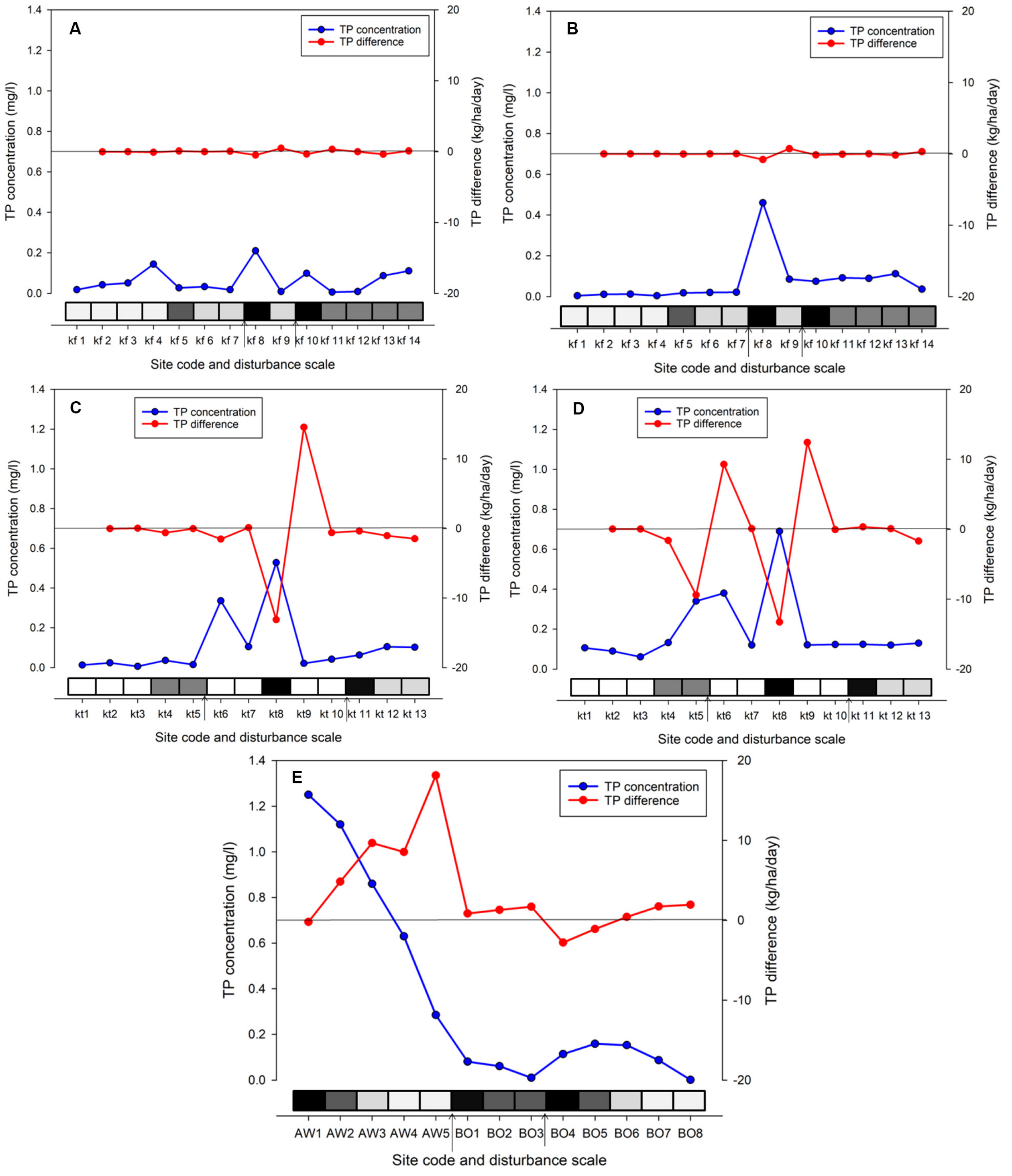

FIGURE 4 | Total Phosphorous (TP) concentration and difference in Kofe **(A)**, Kito **(C)** and Awetu-Boye **(E)** wetlands during wet season and Kofe **(B)** and Kito **(D)** during the dry season. Disturbance condition along the wetland ranged from very low (white) to very high (black). A black arrow indicates a site where a tributary enters into the main stream.

structure, which changes the capacity to retain sediments and nutrients (Gathumbi et al., 2004). Moreover, the deposition of dung and urine during grazing are important sources of nitrogen and phosphorous to surface water (Edwards et al., 2000). Line et al. (2000) indicated that excluding grazing animals from streams in the United States reduced the TSS by 82%, TON by 55% and TP by 78%. Therefore, avoiding the access of cattle to wetlands would be beneficial for water quality. Although

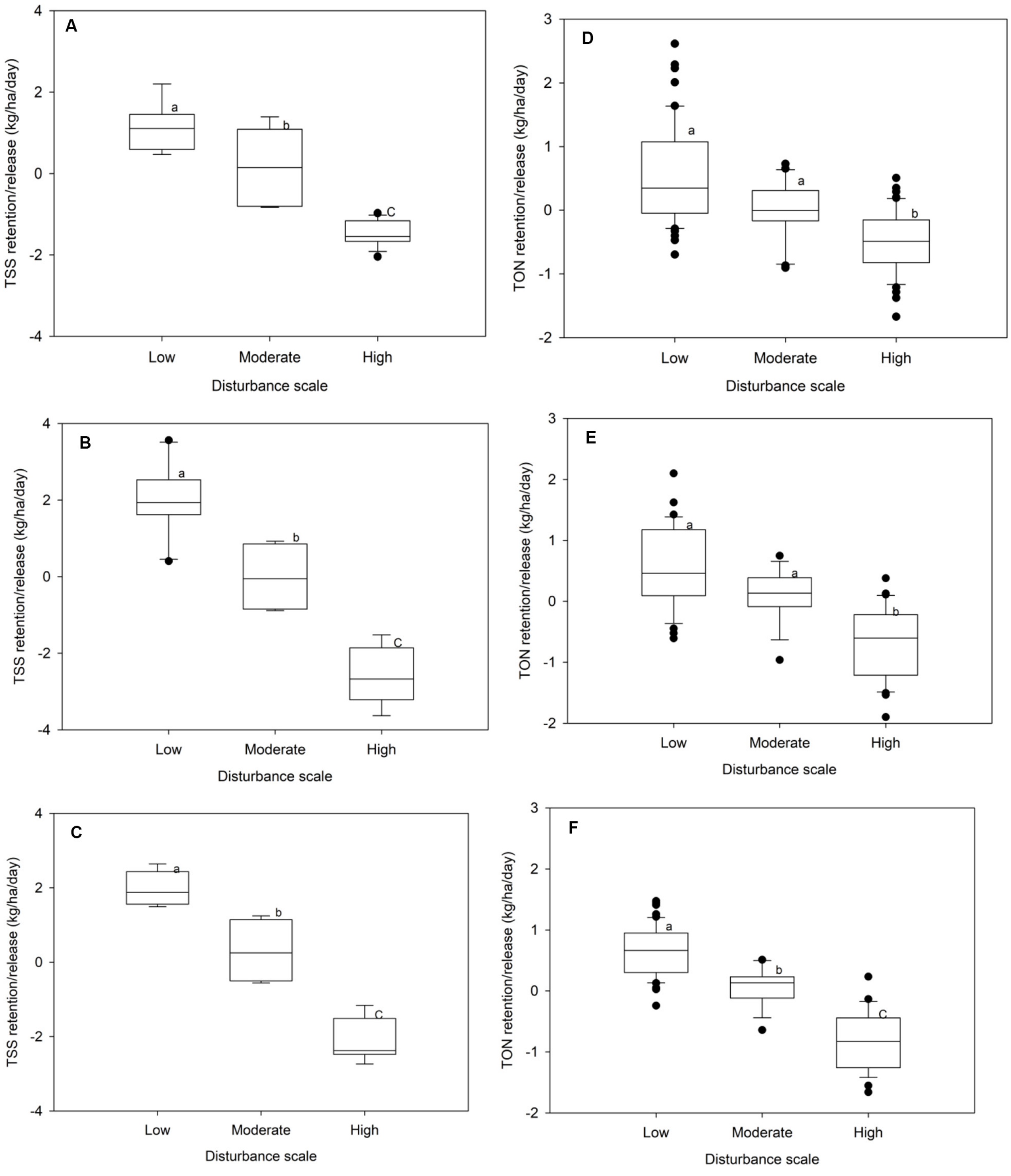

FIGURE 5 | Box- and Whisker plots of the Total Suspended Solids retention log (x + 1) for Kofe **(A)**, Kito **(B)** and Awetu-Boye **(C)** and Total Organic Nitrogen (TON) for Kofe **(D)**, Kito **(E)**, and Awetu-Boye **(F)** in relation to the disturbance classes. The full horizontal line in the box show the median, boxes represent interquartile ranges (25–75% percentiles) and range bars show maximum and minimum values. Statistically significant differences, based on Kruskal-Wallis test ($p < 0.05$), are indicated by letters (a, b, and C).

vegetation clearance was not found to be important in this study, earlier investigations report on the importance of wetland vegetation for nutrient retention (Schoonover et al., 2005). It might be that the reduction of vegetation was not strong enough to have an impact, or that vegetation clearance is very local while the impact of vegetation is acting at a large spatial scale.

Land use changes in the catchment, such as deforestation and agricultural intensification, increase runoff and hence increase the occurrence of peak flow discharges in the rivers, which enhances soil erosion (Van Den Eeckhaut et al., 2009). It has been estimated that about 48% of the Gilgel Gibe catchment is agricultural land (Tefera et al., 2002). Vaithiyanathan and Correll (1992) indicated that the flux of phosphorous associated with runoff from an agricultural watershed was found to be 8 to 10 times higher than that from a similar, but forested landscape. Next to intensive agriculture, landslides are an important source of sediment (Broothaerts et al., 2012). Most of the landslides are located near rivers and at the lowest points in the landscape, which can directly increase the input of sediment to the rivers and consequently increase the sediment load in the rivers and wetlands. These land use changes lead to accelerated rates of soil erosion, which might increase the sediment load in surface waters and cause major modifications to terrestrial carbon, nitrogen and phosphorous cycling (Quinton et al., 2010). Besides the overall negative effect on water quality, high input levels of sediment cause sedimentation and eutrophication problems and reduce the life span of reservoirs. For example, the lifespan of the Gilgel Gibe I reservoir, located 60 km downstream of the studied wetlands, is expected to be reduced by one third due to high sediment transport from the catchment (Devi et al., 2008). Therefore, enhancing TSS retention and nutrient retention capacity of wetlands by reducing anthropogenic pressures is an important step to safeguard both river water quality and the lifespan of the Gilgel Gibe I reservoir.

CONCLUSION AND RECOMMENDATIONS

Freshwater wetlands located in the Awetu sub-watershed have the potential to retain a significant fraction of TSS and nutrients. The highest retention rates were generally measured in wetlands receiving high mass loading rates. On the other hand, wetlands that are affected by a wide variety of human disturbances had higher release of TSS and nutrients. The extent and type of human activities in the catchment (i.e., the land use) can influence the amount of TSS and nutrients released to wetlands. Therefore, reducing anthropogenic pressures such as farming, uncontrolled grazing, clay mining and waste dumping could help to enhance TSS and nutrients retention capacities of wetlands. Therefore, watershed management interventions considering land-use practices in the uplands along with processes occurring in the wetlands and tributaries should be considered for nutrient and sediment management options. Sediment and nutrient retention in wetlands could prevent siltation to eutrophication problem to the downstream surface water resources. This in turn could enhance the ecosystem services provided by aquatic resources.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

SM conceived the main idea of the manuscript, collected and analyzed the data, and wrote the manuscript. LD, PL, WL, PG, and PB contributed to writing the manuscript. All authors read and approved the final manuscript.

ACKNOWLEDGMENTS

The authors are grateful to VLIR-UOS for financing this study. The first author was a recipient of a IUC (Institutional University Cooperation) Ph.D. scholarship from VLIR to carry out this work.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00122/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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in Environmental Science

ORIGINAL RESEARCH
published: 19 August 2020
doi: 10.3389/fenvs.2020.00148

The Impact of Wastewater Discharge and Agriculture on Water Quality and Nutrient Retention of Namatala Wetland, Eastern Uganda

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The Namatala Wetland in Uganda faces severe degradation from agricultural development and urbanization. Besides the Namatala River and tributary rural streams, the wetland receives surface water from Mbale town and wastewater from two sets of wastewater stabilization ponds. The objective of this study was to examine water quality, and sediment and nutrient retention in different land use zones. Five hydrogeomorphic units (HGMUs) were distinguished on the basis of soil, hydrology and land use. HGMUs 1 and 2 in the upstream part of the wetland are characterized by drainage channels and mixed agriculture. HGMU 3 is a wet floodplain with intensive rice farming. HGMU 4 and 5 are permanently wet units in the downstream part of the wetland with moderate rice farming and partly intact papyrus (*Cyperus papyrus* L.) vegetation. Stream discharge was measured, and surface water samples collected, monthly from the river channel, the tributaries, and the five HGMUs from April 2015 to October 2016. Significant differences in total nitrogen (TN), phosphorus (TP) and total suspended solids (TSS) were observed among the streams and among the five HGMUs, with highest concentrations in urban streams and lowest in the main river channel and rural streams. Among the HGMUs, nutrients and TSS were highest within HGMU 3 and lowest in HGMU 1 and 5. Loads of nutrients and sediment into the wetland were greater from the main river channel compared with urban and rural streams. Regressions of net TN, TP, and TSS yields for each HGMU against river discharge showed a net loss of nutrients and sediments in HGMU 3 with the most intensive agriculture, and net retention in HGMUs 4 and 5 which mostly maintain their wetland character. This study shows that sediment and nutrient retention in the downstream part of the wetland compensate for increased export caused by agricultural and urban land use in the middle and upper zones of the wetland, thus maintaining net nutrient retention of Namatala Wetland. However, there is a trade-off between economic development and wetland protection and future management planning should incorporate more sustainable farming practices and improved wastewater treatment.

Keywords: Namatala Wetland, papyrus, sustainable use, water quality, agriculture in wetlands, integrated wetland management

Edited by:
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Specialty section:
This article was submitted to
Freshwater Science,
a section of the journal
Frontiers in Environmental Science

Received: *01 November 2019*
Accepted: *30 July 2020*
Published: *19 August 2020*

Citation:
Namaalwa S, van Dam AA, Gettel GM, Kaggwa RC, Zsuffa I and Irvine K (2020) The Impact of Wastewater Discharge and Agriculture on Water Quality and Nutrient Retention of Namatala Wetland, Eastern Uganda. Front. Environ. Sci. 8:148. doi: 10.3389/fenvs.2020.00148

INTRODUCTION

Conversion of wetlands for agriculture and settlements, and their degradation through pollution with wastewater, are a persistent and global environmental problem (Davidson, 2014). This leads to loss of ecosystem services with negative consequences for people and wildlife (Verhoeven et al., 2006; Díaz et al., 2015; Ramsar Convention on Wetlands, 2018). In Sub-Saharan Africa, although many countries are signatories to the Ramsar Convention on Wetlands and have national policies for wetland protection (Gardner et al., 2009; Dini and Everard, 2018), loss and degradation of wetlands continue. Agriculture is one of the most important drivers of wetland loss (van Asselen et al., 2013; Ramsar Convention on Wetlands, 2018), with most countries having policies for expanding agricultural production (OECD/FAO, 2016). The need to produce food is increasing, and a projected growth of the population on the African continent to 2.1 billion people by 2050 drives a policy conflict between protecting wetlands and achieving food security.

Uganda was one of the first African countries to recognize the importance of wetland ecosystem services by developing a wetland policy and designating Ramsar sites. The policy aims at ensuring that there is no drainage of wetlands, that activities in and around wetlands are non-destructive, and that developments are subject to environmental impact assessment and audits (Mafabi, 2000, 2018). Despite this, sustainable management of Ugandan wetlands has often floundered in the face of local pressures. Striking a balance and accepting trade-offs between protection and exploitation of wetlands is often restricted by lack of knowledge on wetland function. More information is needed on land use that contributes to nutrient and sediment loads (Namaalwa et al., 2013) and the capacity of wetlands to remove nutrients from wastewater (Kansiime and Nalubega, 1999; Bateganya et al., 2015). A lack of government capacity in implementing policy exacerbates the problem (Ostrovskaya et al., 2013). More knowledge about the impact of economic development and land use change would help wetland users and policy makers view patterns and impacts more clearly, prioritize vulnerable zones of the catchment, and implement sustainable land use planning and practice.

Several processes contribute to retention of sediment and nutrients in wetlands, including sedimentation, uptake and storage in vegetation, adsorption to soil, and gaseous losses to the atmosphere. Their relative importance depends on environmental conditions, soil characteristics, and hydrology (Burt and Pinay, 2005; Noe and Hupp, 2007; Lohse et al., 2009; Pärn et al., 2012). Variable land use and seasonal climatic patterns in small wetland areas provide scale-dependent effects on biophysical processes (Jung et al., 2008; Park et al., 2011; Uwimana et al., 2017). Translating knowledge of hydro-ecological processes into maintenance of ecosystem services and conservation of biodiversity is needed as an evidence-based approach to managing pressures from wastewater, food production and livelihoods (Biggs et al., 2015).

Different zones of a wetland catchment that are subject to different intensities of anthropogenic pressure can be expected to vary in their contributions to nutrient and sediment retention (Baker et al., 2006; Noe and Hupp, 2007). This raises questions about the overall functioning of the wetland. Can the loss of retention in one zone be compensated by retention in another? How does this overall functionality depend on hydrological connectivity and flow paths? Can these functions be quantified to find a sustainable balance between the use of the wetland ecosystem (e.g., for agricultural production) and a desirable level of ecological functioning? For Namatala Wetland in Uganda, we hypothesize that retention in the zones influenced by agriculture and wastewater is reduced compared with zones where the integrity of the original wetland and its natural processes (with papyrus vegetation and regular flooding) are still intact. The overall objective of this study was to examine water quality and estimate sediment and nutrient loads across upstream and downstream zones with different anthropogenic pressures (wastewater discharge and agriculture) in a tropical wetland and river system. Specific objectives were: (1) to describe discharge and water quality in river and wetland in relation to seasonal and land use variation; (2) to estimate loads of sediment and nutrients (nitrogen, phosphorus) from the river and its tributaries; and (3) to compare different wetland land use zones in terms of sediment and nutrient retention.

MATERIALS AND METHODS

Study Area

The Namatala Wetland is part of the Doho-Namatala Wetland System within the Lake Kyoga Basin. It lies along the main Namatala River with a stretch of about 31 km from upstream to downstream, and a surface area of 113 km^2 (**Figure 1**). The average rainfall in the wetland is 1,300 mm per year in a bi-modal pattern, with peaks in April-June and September-November. Ambient air temperature is in the range of 20–30°C. The wetland has an elevation range from 1,150 m upstream to 1,060 m downstream. The geology of the area comprises Pre-Cambrian rock, mainly granites (WMD, 2008). The wetland soils consist of clay loam in the central area and sandy loam in the swampy lowlands (WMD, 2008; Kayendeke and French, 2019). The major tributaries are three perennial streams, Nabuyonga, Nashibiso, and Nambale/Ndukwe, which receive water from other intermittent streams and ephemeral channels (**Figure 1**). In addition, the wetland receives surface water from two urban streams (Budaka and Nashibiso) draining the upstream catchment and the urban center of Mbale town, including the wastewater discharge from two sets of wastewater stabilization ponds (WSPs) operated by National Water and Sewerage Corporation (NWSC), Uganda.

The wetland is located in a densely populated region (average 577 inhabitants km^{-2}) within the districts of Mbale, Butaleja, Budaka, Bududa, Sironko, and Pallisa (UBOS, 2014). Mbale district has a population of 488,900, with 93,000 people residing in Mbale town which has an expanse of informal settlements along Namatala River and Nabuyonga, Budaka and Nashibiso streams (Cities Alliance, 2015). Open waste disposal is common within these settlements. Only 3.7% of the population is served by the sewer network. Because of old sewer mains, ingress of storm

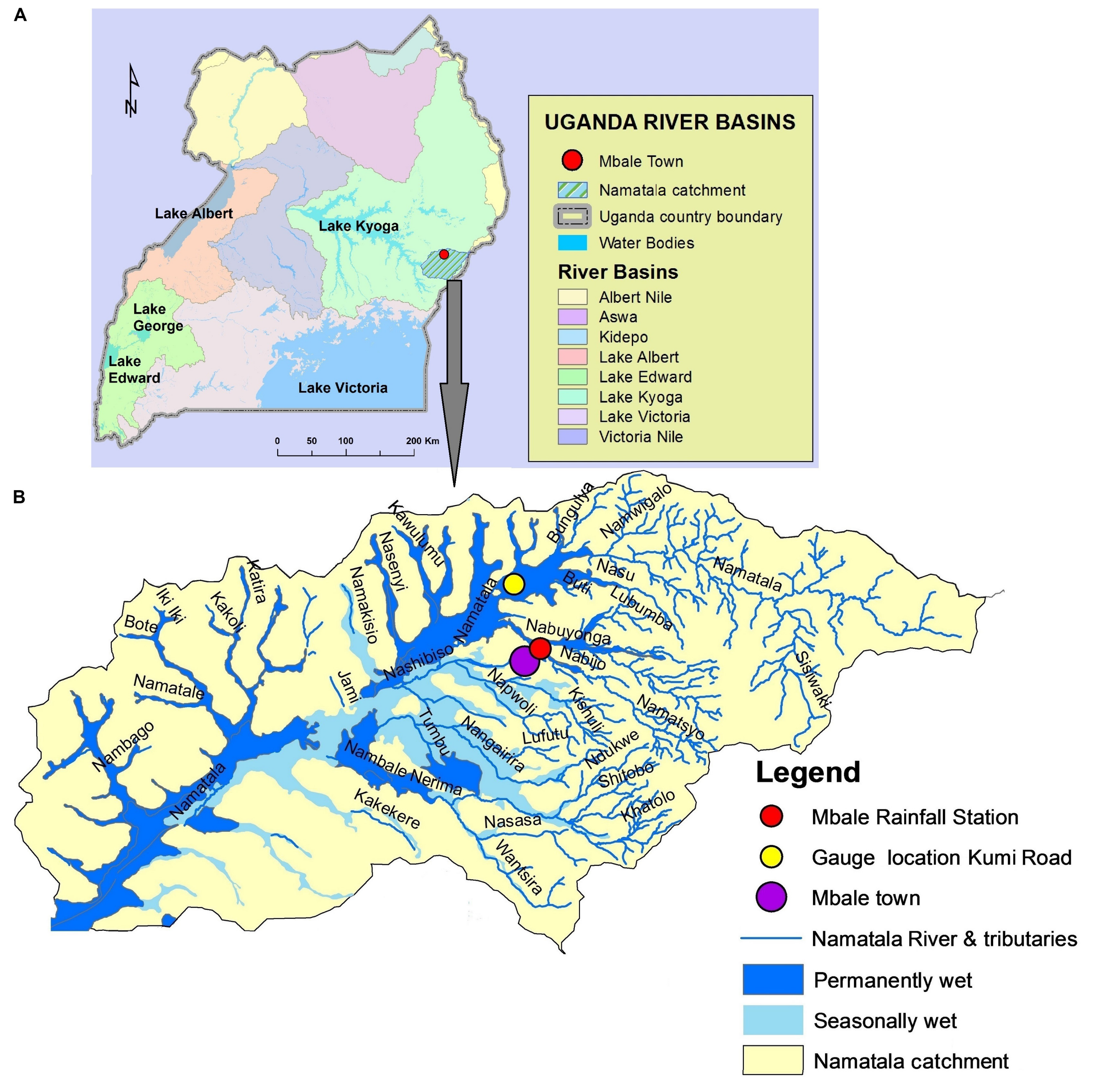

FIGURE 1 | (A) Location of Mbale town and Namatala Wetland within Uganda; **(B)** Drainage system of Namatala Wetland. Data source: Mapping and Inventory Centre, National Forestry Authority Uganda, 2005. Maps produced by authors.

water in the pipe network is common, resulting in overloading of the WSPs. Final effluent has been reported to have a COD of 300 mg L^{-1}, BOD of 180 mg L^{-1}, and fecal coliforms of 26,000 CFU (100 mL)$^{-1}$ (NWSC, 2017).

The population around the wetland depends on agriculture as the main source of livelihood. The extent of wetland area cleared for farming has been increasing over the years. In the upper part of the wetland, about 100 km^2 was cleared for wetland farming between 1990 and 2010 (NFA, 2005; Namaalwa et al., 2013). Agricultural practices include surface drainage, soil compaction and removal of wetland vegetation. The original papyrus vegetation (*Cyperus papyrus* L.), which is known for its high productivity and storage capacity for nutrients (Kansiime et al., 2007; van Dam et al., 2014), has declined. This has created concerns about the impact of the land use change on sediment and nutrient retention in the wetland and on downstream water quality.

Currently, the seasonally wet zones in the upper wetland comprise subsistence agriculture with cultivation of rice, yams, maize, bananas, and sweet potatoes. The middle part of the wetland is used mainly for commercial rice farming in two seasons (February-July and August-January). Land preparation at the beginning of each season includes tillage, creation of channels and ditches for irrigation of the nursery beds, and construction of compacted dikes to ease access to the farms and regulate water flows. The wettest lower part of the wetland still has a considerable area with intact papyrus vegetation.

Field Sampling Design and Selection of Sampling Points

The wetland was divided into five hydrogeomorphic units (HGMUs) according to soil, hydrology and land use (**Figure 2**; Namaalwa et al., 2013). HGMUs 1 and 2 are located in the upstream part of the wetland, with a catchment that includes Mbale town and settlements in the neighboring areas of Mutoto, Bungokho, Bumageni, Nambale, and Nakaloke. HGMUs 1 and 2 have straightened river channels, compacted surface soils, high surface water flow rates, and low connectivity with, or inundation from, the main river. HGMU 3 is the mid-floodplain of the wetland, characterized by intensive rice farming. The major surface inflow into HGMU 3 is the Namatala River channel flowing out of HGMU 1 and 2. Within HGMU 3, intensive rice farming involves excessive tillage, tile drainage, diversion of surface water and high surface water flow rates. HGMUs 4 and 5 are permanently wet units in the downstream part of the wetland with moderate rice farming, some soil tillage in rice fields, and diversion of surface water flow. Partly intact wetland vegetation maintains a stronger wetland character compared with upstream HGMUs (see **Table 1**).

The wetland surface inflows were grouped into three categories, determined by the immediate catchment: (1) Namatala River, with seven sampling points (Kumi Road, Kamonkoli, Jami, Naboa, Sapiri, Kazinga, and Irabi) along the main river channel as it flows from upstream to downstream; (2) rural streams, Nabuyonga, Nashibiso-1, and Ndukwe, which are natural tributaries of Namatala River fed by smaller, often ephemeral streams; and (3) urban streams, also tributaries of the river, two of which (Budaka and Nashibiso-2) receive untreated domestic and industrial wastes from Mbale town, and the other two (Namatala WSP and Doko WSP channels) that discharge effluent from the two sets of WSP systems. A detailed layout and characteristics of the HGMUs are given, respectively, in **Figure 2** and **Table 1**.

Precipitation and Discharge

Daily precipitation data recorded at the weather station in Mbale town, and discharge data recorded from the automatic gauge station (**Figure 2**) were obtained from the Directorate of Water Resources Management, Entebbe, for the period 2003–2016. Data was processed to generate mean monthly total rainfall and discharge. To estimate the contribution of groundwater to the wetland's water resources, baseflow separation was carried out using the method developed by WMO (2008), and a 16 years long daily time series (period 2000–2015) of discharge at the Kumi Road gauge (**Figure 2**). The long-term average value of the Base Flow Index (BFI), which is the ratio of the cumulative volumes of baseflow and total discharge, was estimated. The quality of the groundwater was investigated by comparing the separated hydrograph with the monthly variations in water quality (especially nutrients) at Kumi Road.

Data to support calculation of discharge in the other sampling stations in Namatala River channel and in the tributary streams were collected monthly from April 2015 to October 2016. Flow velocity was measured at 25, 50, and 75% of the total stream width using a portable velocity flow meter with electromagnetic sensor (model FH950, Hach Company, Colorado, United States). At the same time, width and depth of the wetted perimeter were measured. Discharge was calculated using the velocity-area method (Herschy, 2009).

Water Quality

Samples for measuring water quality were collected monthly from April 2015 to October 2016 at the sampling points (**Figure 2**). For the river and tributaries, samples were taken using an alpha horizontal water sampler (Science First/Wildco, Yulee, Florida, United States) to make a composite sample from different depths (surface, middle and bottom). Because of the low water levels at the wetland points, grab samples were taken by filling the bottle beneath the surface of the water.

A photometric method was used to determine total suspended solids (TSS) of unfiltered samples using a spectrophotometer (DR 6000, Hach Company, Colorado, United States). Temperature, pH, electrical conductivity (EC), and dissolved oxygen concentration (DO) were measured *in situ* using a multi-parameter water quality meter with probe (Hydrolab Quanta, Hydrolab Corporation, Texas, United States). Water samples were placed in cool boxes kept at below 4°C and transported to the NWSC central laboratory in Bugolobi, Kampala, for analysis of nitrogen and phosphorus following standard methods (APHA, 2005). For nitrogen, ammonium (NH_4-N; sodium salicylate and hypochloride method), nitrate (NO_3-N; sodium salicylate method), nitrite (NO_2-N; sulfanilamide and N-naphthyl-(1)-ethylendiamin-dihydrochlorid method), and total nitrogen (TN; alkaline persulfate digestion) were determined. For phosphorus, soluble reactive phosphorus (PO_4-P; ascorbic acid method) and total phosphorus (TP; acidic persulfate digestion) were determined.

Sediment and Nutrient Loads in Surface Inflows

Total monthly sediment and nutrient loads at each river and stream sampling point were calculated by relating monthly discharge and water quality measurements to the river discharge measurements at the Kumi Road gauging station (based on Wollheim et al., 2005). First, we used regression equations to relate the measured discharge to corresponding discharge recorded at the gauging station for each sampling occasion. Regression equations (covering samples from the whole 19 month period, R^2 in the range 0.82–0.97; **Supplementary Table 3**) were used to estimate discharge at each sampling point for every day of the sampling period (except for the months August-November 2015, when the gauging station

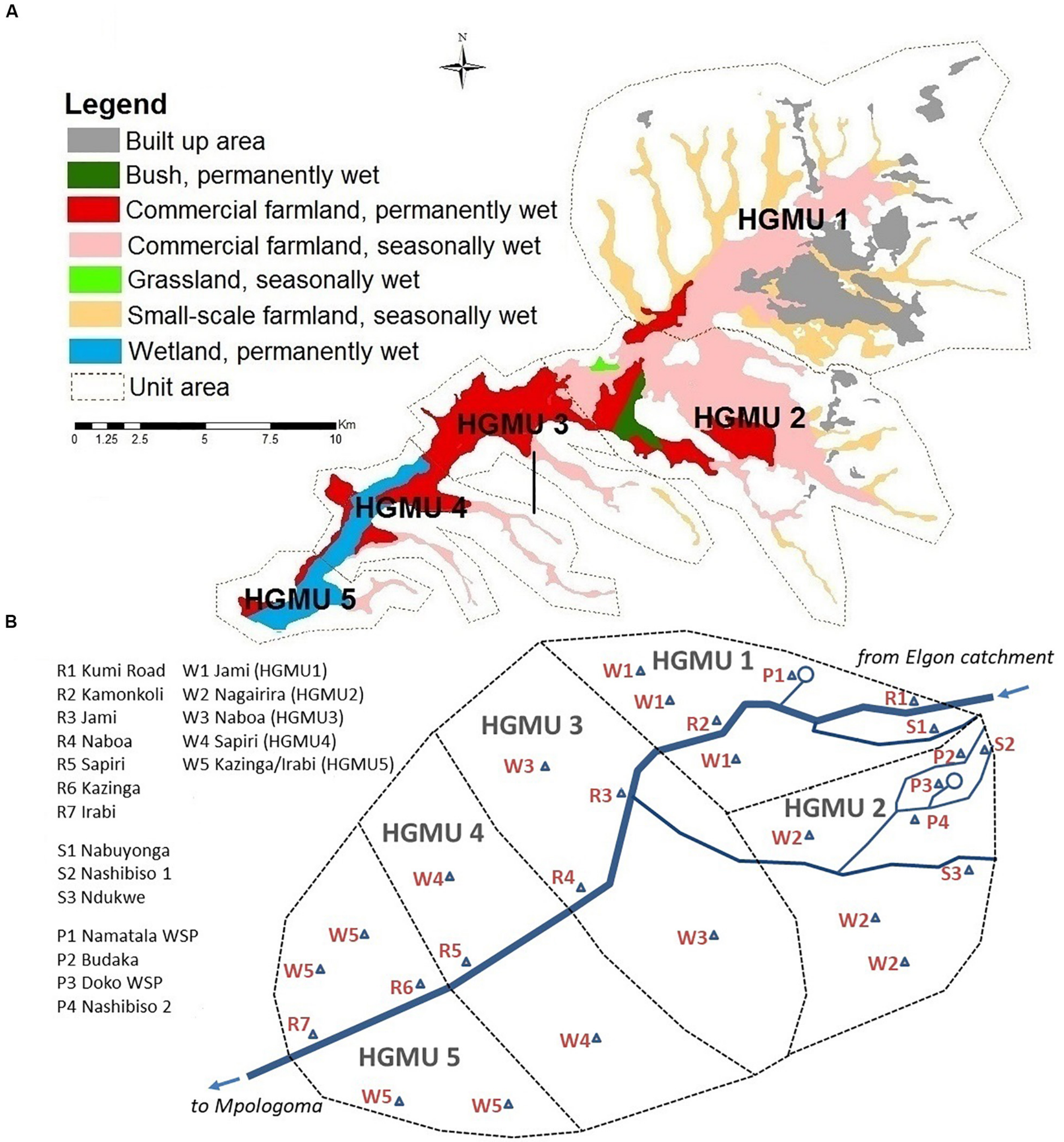

FIGURE 2 | (A) Layout of hydrogeomorphic units (HGMUs); and **(B)** schematic map of sampling points in Namatala Wetland, Uganda. Inflow and outflow points for calculation of net yields were: HGMU 1: P1, R1, and S1 (in) and R2 (out); HGMU 3: R3 (in) and R4 (out); HGMU4: R4 (in) and R5 (out); and HGMU5: R5 (in) and R7 (out) (see legend for codes; R, river; S, rural streams; P, polluted streams; W, wetland). For HGMU 2, no net yield calculation was done because no outflow location was available. WSP, wastewater stabilization pond. For further explanation, see text. Data source for **(A)** Mapping and Inventory Centre, National Forestry Authority Uganda, 2005. Map produced by authors.

was not working). Then, regressions were calculated between measured concentrations of TSS, TP and TN and measured discharge at each sampling point. These regressions (R^2 in the range 0.71–0.96 for TSS; 0.80–0.93 for TP; 0.61–0.90 for TN; **Supplementary Table 4**) were then used to estimate daily concentrations of TSS, TN, and TP from the estimated daily discharge values at each sampling point. Finally, monthly TSS, TP, and TN loads (metric tonnes month^{-1}) were calculated for all river and stream sampling points by multiplying daily discharge and concentration estimates, and summing for each

TABLE 1 | Characteristics of the hydrogeomorphic units (HGMUs) in Namatala Wetland.

HGMU	Area and physical features	Surface water flows and regime	Soil texture	Land use
HGMU 1	3874 ha seasonally wet	River: Namatala Rural streams: Nabuyonga Urban streams: Namatala WSP	Clay	Subsistence mixed agriculture; Crops include cassava, sugarcane, tomatoes, bananas, yams, maize
HGMU 2	3816 ha seasonally wet	Rural streams: Nakibisho-1, Ndukwe Urban streams: Budaka, Nakibisho-2, DOKO WSP	Sandy clay	Subsistence mixed agriculture; Crops include cassava, sweet potatoes, tomatoes, bananas, yams, maize
HGMU 3	1387 ha permanently wet	River: Namatala	Sandy clay	Predominantly rice
HGMU 4	1509 ha permanently wet	River: Namatala	Sandy clay	Rice (65%); Papyrus and sedges (35%)
HGMU 5	679 ha permanently wet	River: Namatala	Sandy clay	Papyrus and sedges; Crops (sugarcane, rice, maize) occupy 36% of the unit

For river network (see ***Figures 1B**, **2B****). Soil data were collected under the EU-FP7 WETwin project in 2010.*

month. The significant linear regressions across a wide range of discharge values with high R^2-values provided confidence in these monthly load estimates.

Net Yields as Estimate of Sediment and Nutrient Retention

From the loads at each stream sampling point, net yields (in tonnes month^{-1} km^{-2}) were calculated for each month in HGMUs 1, 3, 4, and 5 as the difference between total incoming and outgoing load (based on the sampling points in the inlets and outlets of these HGMUs; see **Figure 2**), divided by the surface area of the HGMU (in km^2), as follows:

HGMU1: [Load (Kumi Rd) + Load (NamatalaWSP) + Load (Nabuyonga) – Load(Kamonkoli)]/38.74
HGMU3: [Load (Jami) – Load (Naboa)]/13.87
HGMU4: [Load (Naboa) – Load (Sapiri)]/15.09
HGMU5: [Load (Sapiri) – Load (Irabi)]/6.79

The calculation could not be done for HGMU 2 because it did not have a suitable outflow point (**Figure 2**). Positive values of these net yields are interpreted as a measure of retention, whereas negative values suggest export of sediment or nutrients from the HGMU.

Data Analysis

To compare HGMUs and stream types, linear mixed effects ANOVA models were formulated using HGMU or stream type, month and their interaction as fixed variables, and individual sampling points as a random effect. The random effect accounted for the dependence of the repeated measurements (Everitt and Hothorn, 2010). Random intercept models were compared with models without the random component, and the model with the lowest AIC (Akaike Information Criterion) was selected. Mean values of water quality variables were compared among the HGMUs and among stream types (only the tributaries, as the river sampling points were not replicated) using least square means with Tukey adjustment. River water quality samples were compared from upstream to downstream using a non-parametric pairwise test (Wilcoxon signed rank test). Monthly net yields in HGMUs 1, 3, 4, and 5 were related to mean inflow into the respective HGMU using simple linear regression. All calculations were done using function wilcox.test for the signed rank test, function lme for estimating the mixed models, function lsmeans for *post-hoc* analysis, and function lm for the regression (for the load and net yield calculations), all part of R software version 3.3.1 (R Core Team, 2018). Significance is reported at $p < 0.05$, unless stated otherwise.

RESULTS

Precipitation and Discharge

During the study period, precipitation ranged from almost zero in the very dry months of February and July of 2016 to peaks of 130-150 mm in May-June 2015, 230 mm in October 2015, and 160-170 mm in April-May 2016 (**Figure 3**). These rainfall peaks were reflected in the highest discharge observed in Namatala River between April and June, and between August and October in both years (**Figure 4A**). The highest discharge of about 22,000 m^3 h^{-1} was recorded at Naboa in HGMU 3, and at Jami after the confluence of Namatala River with the Nabuyonga and Ndukwe streams (**Figure 5**). This discharge was about three times higher than that recorded at Kumi Road, the upstream point of the river. Maximum discharge in the tributaries was on average 1,000^{-1},100 m^3 h^{-1} in the rural streams during the rainy periods in 2016. The urban streams had the lowest peak discharge, at 200–300 m^3 h^{-1} (**Figure 4B**).

Figure 6 shows the separated hydrograph of Namatala River at Kumi Road for the experimental period, along with concentrations of nitrogen and phosphorus. The BFI value estimated for the Namatala River at Kumi Road was 0.605, which means that, in the long run, about 60% of the inflow into Namatala Wetland at Kumi Road originates from the groundwater of the upstream catchment. Peaks in nutrient concentrations coincided with waves of surface runoff which washed organic and inorganic substances into the river, mainly from agricultural lands. By contrast, nutrient concentrations were low during baseflow-dominated periods.

Spatial and Temporal Water Quality Variation of Streams

Water quality in the Namatala River changed significantly from upstream to downstream sampling points, with the strongest changes observed from Jami to Naboa (the sampling point just downstream of the rice farming area in HGMU 3), and from Naboa to Sapiri (where the more natural part of the wetland starts). TSS and EC (**Figures 5B,C**) were significantly higher in Naboa than in Jami (upstream) and Sapiri (downstream). For nutrients (TP, PO_4-P, TN, NH_4-N), a similar significant peak in concentrations at Naboa occurred (**Figures 5E,F**). DO had the

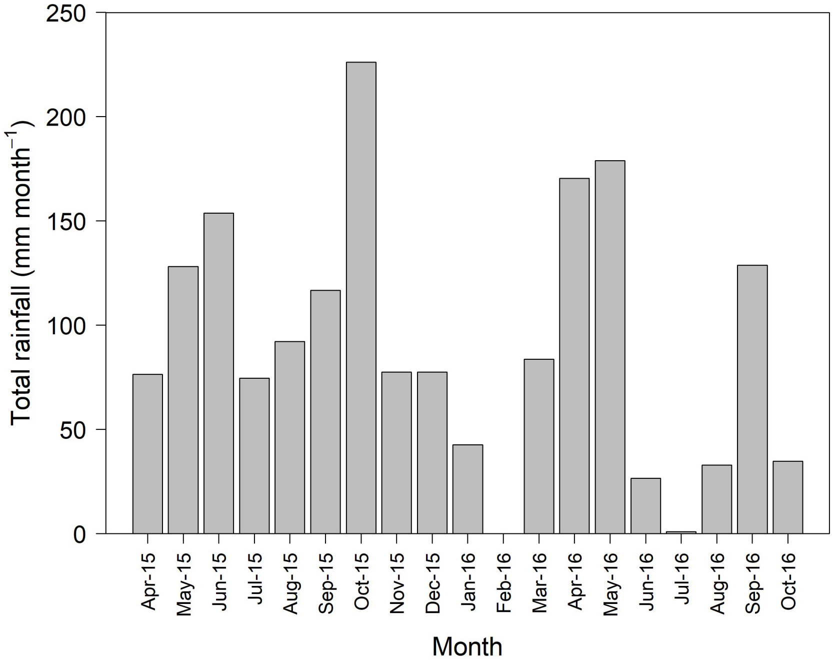

FIGURE 3 | Total monthly rainfall at the weather station in Mbale, Uganda, during the study period April 2015–October 2016. No or very little rainfall occurred in the area in February and July 2016. Data source: Directorate of Water Resources Management, Entebbe.

opposite pattern, with a significant drop from around 6 mg L^{-1} in Kamonkoli and Jami to 3.4 mg L^{-1} in Naboa, and further significant decreases in Sapiri and Kazinga (all comparisons Wilcoxon paired *t*-test, $p < 0.001$; see **Supplementary Table 1**). Nitrite (NO_2) and nitrate (NO_3) concentrations decreased significantly from Jami to Naboa and from Naboa to Sapiri.

Water quality in the tributaries exhibited clear differences among stream types and seasons (**Figure 7**), but with significant interactions between stream type and month for EC and nutrients (ANOVA; see **Supplementary Table 2** for all means and variation). Mean EC over the 19-month sampling period was 111 and 235 μS cm^{-1} in river (Kumi Road station) and rural streams, respectively, with low seasonal variation. In the urban streams, EC was significantly higher (mean value 898 μS cm^{-1}), with peaks in the dry seasons (July 2015, February 2016, and June-August 2016). Mean TSS ranged from 25 to about 250 mg L^{-1}, with differences in mean TSS not significant among tributaries. Variation in TSS was mostly related to seasonal differences, with peaks in the periods of high discharge (May-June 2015, October 2015, April-May 2016, and September 2016). Similarly, nutrient concentrations (NH_4-N, TN, PO_4-P, and TP) showed seasonal peaks during the wet periods, with significantly higher nutrient concentrations in the urban streams. Mean DO concentrations were lowest in the urban streams (1.3 mg L^{-1}), compared with the river (5.7 mg L^{-1} at Kumi Road station) and rural streams (3.2 mg L^{-1}). pH was highest in urban streams (mean 8.4) and lowest in the river (mean 7.7). Mean temperature ranged from 24.7°C in rural streams, to 25.2°C in both the river and in urban streams. There was a slight seasonal range of 2–3°C (see **Supplementary Table 6**).

Spatial and Temporal Water Quality Variation Among HGMUs

High spatial variation in DO, EC, pH, and TP was observed among the wetland units (**Figure 8**). Mean DO decreased significantly from upstream to downstream HGMUs, with highest DO in HGMU 1 and lowest values in HGMUs 4 and 5. For EC and TP, the lowest mean values were observed in HGMUs 1 and 5, and highest values in HGMU 3. TSS, pH and nutrients were significantly higher in HGMUs 3 and 4 than in the other HGMUs, except for $N0_3$-N which was significantly lower in HGMUs 3 and 4 than in the other HGMUs. In HGMUs 3, 4, and 5, total nitrogen consisted of NH_4-N for about 70% of the samples, whereas in HGMUs 1 and 2 this was only 30%. A slight seasonal effect was observed with a decrease of pH in the wet seasons (April-June, October-December), possibly due to increased discharge. Fluctuations in EC were observed over the entire sampling period; however, values were consistently higher for HGMUs 2 and 3. EC values ranged from 174 to 243 μS cm^{-1} in HGMU 2 and from 180 to 338 μS cm^{-1} in HGMU 3. Within each HGMU, peak values of EC were recorded during the dry months (July-August, January-February). Mean temperatures were slightly lower in HGMU 4 (23.9°C) and 5 (23.8°C) and higher in HGMU 1 and 2 (25.0°C), with an average of 24.7°C for HGMU 3.

Sediment and Nutrient Loads

Seasonal trends were also observed in TSS, TP, and TN loads of all surface inflows with high loads during the peak rainfall period of April-June (especially in 2016), and a reduction in loads during

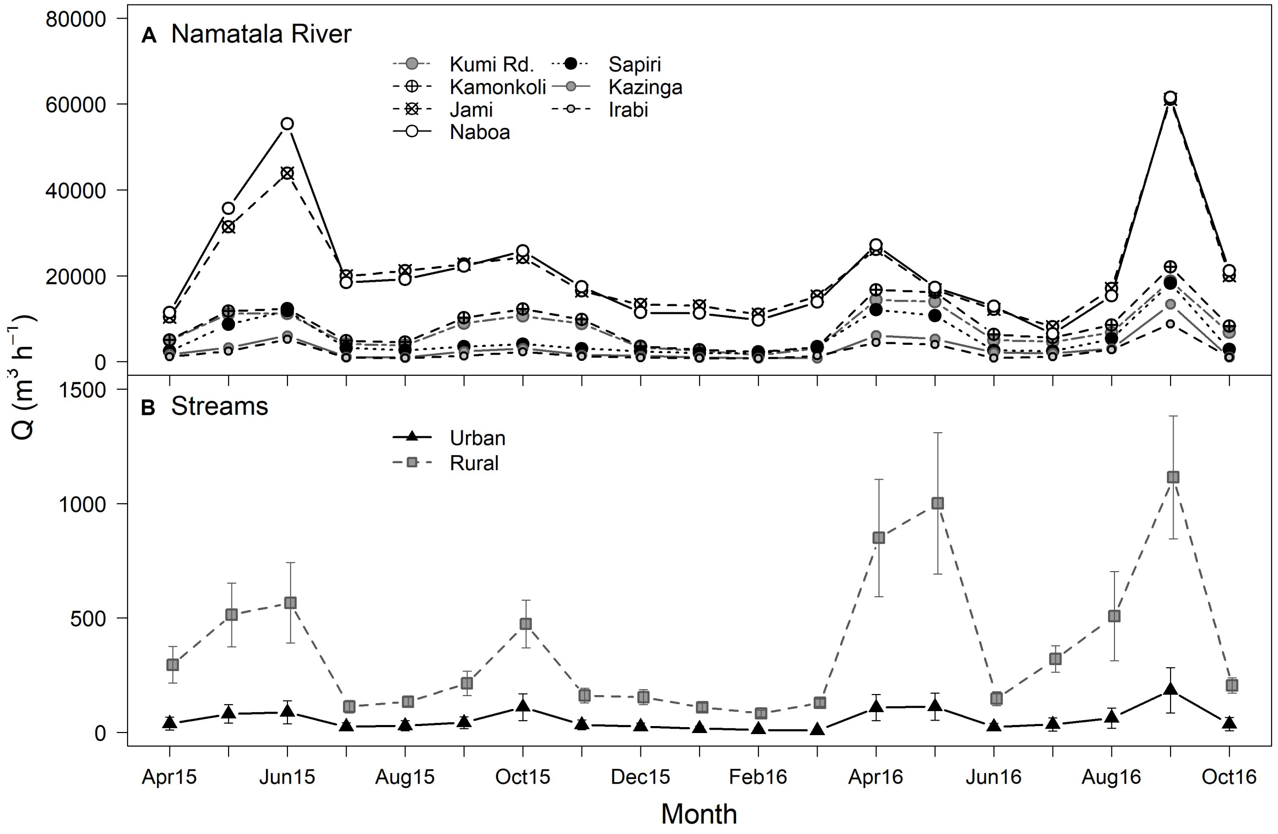

FIGURE 4 | Discharge in m^3 h^{-1} measured monthly in Namatala Wetland for the period April 2015–October 2016, with **(A)** seven sampling points in Namatala River; and **(B)** mean values for the four urban streams (n = 4) and three rural streams (n = 3). Error bars indicate standard error.

other months of the year (**Figure 9**). The loads of TSS, TP and TN in the main river were one (TP, TN) to two (TSS) orders of magnitude greater compared with rural and urban streams, with the lowest loads recorded among urban streams for the entire period. Along the main river channel, TSS loads decreased from the upstream point (Kumi Road) through the mid-stream sub-catchment (Naboa, Sapiri) to the downstream points (Kazinga, Irabi). Nutrient (TN and TP) loads, however, were highest in Jami (after the confluence of Ndukwe stream with the river), and especially Naboa (just downstream of HGMU 3).

Net Yields for HGMUs With Different Land Use

Positive net yields were observed mainly in downstream HGMUs 4 and 5, and negative to near-zero yields in the upstream HGMU 1 and midstream HGMU 3. The highest mean net TSS yields were found in HGMU 4 (331 t km^{-2} month^{-1}) and HGMU 5 (72 t km^{-2} month^{-1}), and the lowest in HGMU 3 (-160 t km^{-2} month^{-1}). Similarly, mean net yields of TP and TN were highest in HGMU 4 (3.3 t km^{-2} month^{-1} for TP and 3.7 t km^{-2} month^{-1} for TN) and lowest in HGMU 3 (-1.3 t km^{-2} for TP and -1.5 t km^{-2} for TN). Net yields in HGMUs 4 and 5 showed significant positive linear relationships with mean monthly inflow (all R^2 = 0.85 or higher), suggesting retention of sediment and nutrient in these downstream HGMUs. In HGMUs 1 and 3, this relationship had a significant negative slope suggesting export of sediment and nutrients in these highly converted HMGUs (except for net TN yield in HGMU1 where R^2 = 0.38; **Figure 10**, see also **Supplementary Table 5**).

DISCUSSION

Lake Kyoga and its connected wetlands drain the groundwater bodies underneath the surrounding hills and high grounds, and water flow in the opposite direction is unlikely (Owor et al., 2011; Kayendeke and French, 2019). The estimated BFI value in this study was practically identical to the BFI calculated for the Namatala River by Rugumayo and Ojeo (2006), who also calculated BFIs for other rivers in the Kyoga basin and derived similar, or even higher, values (e.g., BFI was 0.875 for Mpologoma River). The high BFI values mean that groundwater inflows from the hills and mountains into the wetlands are high compared with surface runoff inflows. To assess the influence of these groundwater inflows on surface water quality in the Namatala Wetland, we checked the water quality of the river during baseflow periods, such as February 2016. Concentrations of dissolved inorganic nutrients (NH_4-N and PO_{4-}P), as well as concentrations of TSS, TN, and TP were the lowest in this month

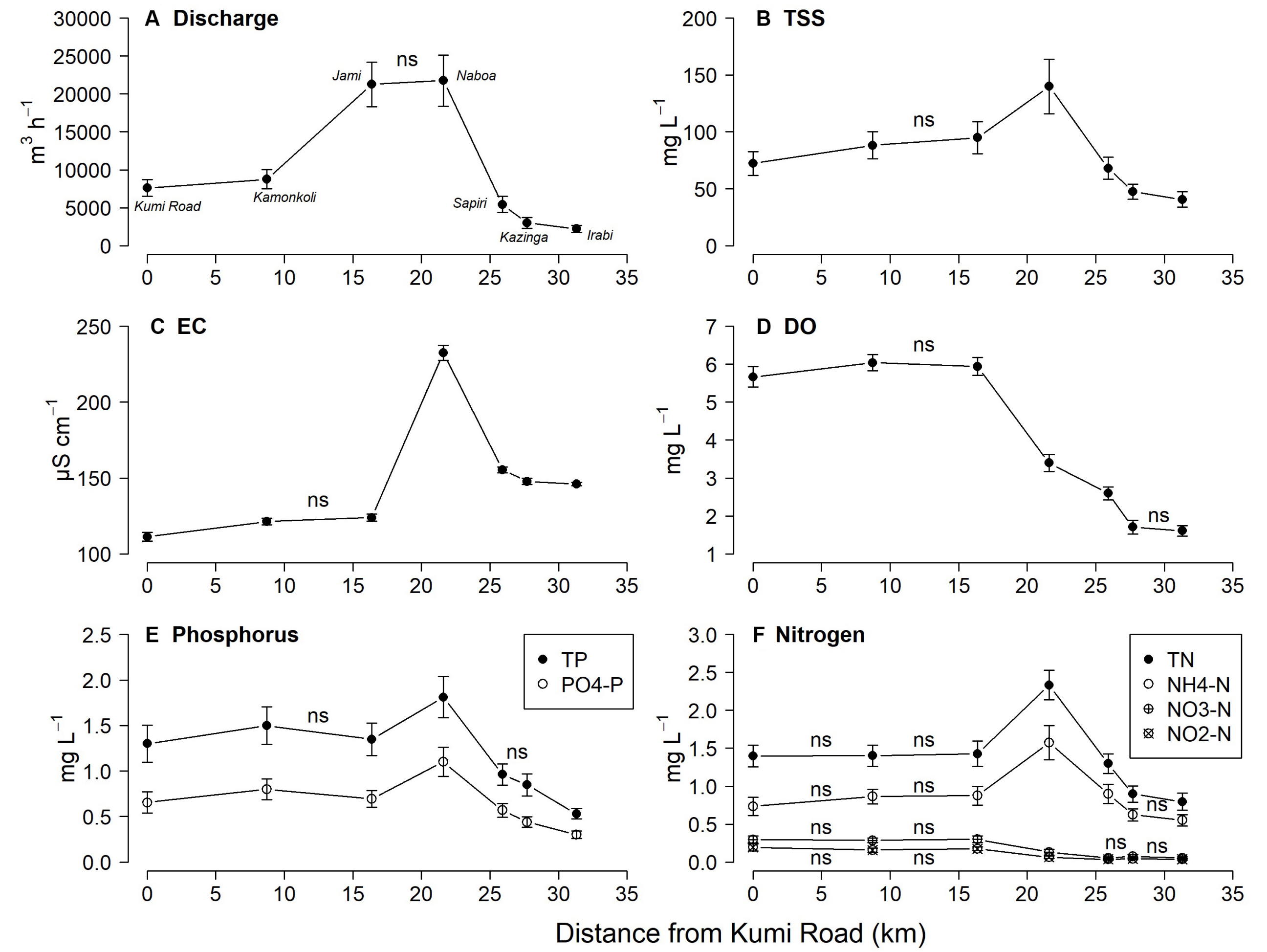

FIGURE 5 | Variation of discharge and water quality in the main channel of Namatala River from upstream to downstream for the period April 2015 – October 2016. **(A)** Discharge; **(B)** Total suspended solids (TSS); **(C)** Electrical conductivity (EC); **(D)** Dissolved oxygen (DO); **(E)** Total and soluble reactive phosphorus; **(F)** Total nitrogen, and ammonium, nitrate and nitrite nitrogen. Names of the sampling points are indicated in panel **(A)**. Data points are means of 19 monthly measurements; error bars indicate standard error. Differences between consecutive sampling points are significant (Wilcoxon signed rank test, *P* at least < 0.05) unless indicated by "ns" (not significant).

compared with the rest of the monitoring period. This means that groundwater, although contributing significantly to the wetland's water resources in quantitative terms, does not carry considerable amounts of nutrients into the wetland. The bulk of organic and inorganic nutrient inputs come with surface runoff during the flood periods, as shown by the coincidence of flood periods with the peaks of nutrient concentrations.

There were clear differences in water quality among the Namatala River and its rural and urban tributaries, with a strong influence from the different types of land use in the wetland. The highest TSS and nutrient concentrations and EC were observed in the urban streams in HGMUs 1 and 2, which also showed strong seasonal differences in EC and nutrient concentrations. This seasonal dynamic of nutrient flow from urban streams is influenced by the characteristics of their catchment. Open waste disposal, limited sewer network coverage, and storm water and sewage overflow during rainfall periods lead to overflow of nutrients into the streams. The runoff resulting from soil compaction, stream widening, diversion, and straightening in the upper catchment of Namatala Wetland mobilizes sediments and nutrients from impervious surfaces and farms into receiving streams (Recha et al., 2012; Uwimana et al., 2017). The presence of inorganic nitrogen (mainly NH_4-N) and orthophosphate as main forms of TN and TP, respectively, is characteristic of the influence from the urban catchment, as shown in other studies on the impact of land use on water quality (Nyenje et al., 2010; Haidary et al., 2013). However, these higher concentrations in the urban streams did not have a strong impact on the nutrient concentrations after the confluence with the river in Jami, which were not significantly different from those in Kamonkoli. This was confirmed by the load calculations which showed much higher sediment and nutrient loads in the river than in the tributaries. While their impact on river water quality is limited, locally these polluted streams may lead to environmental

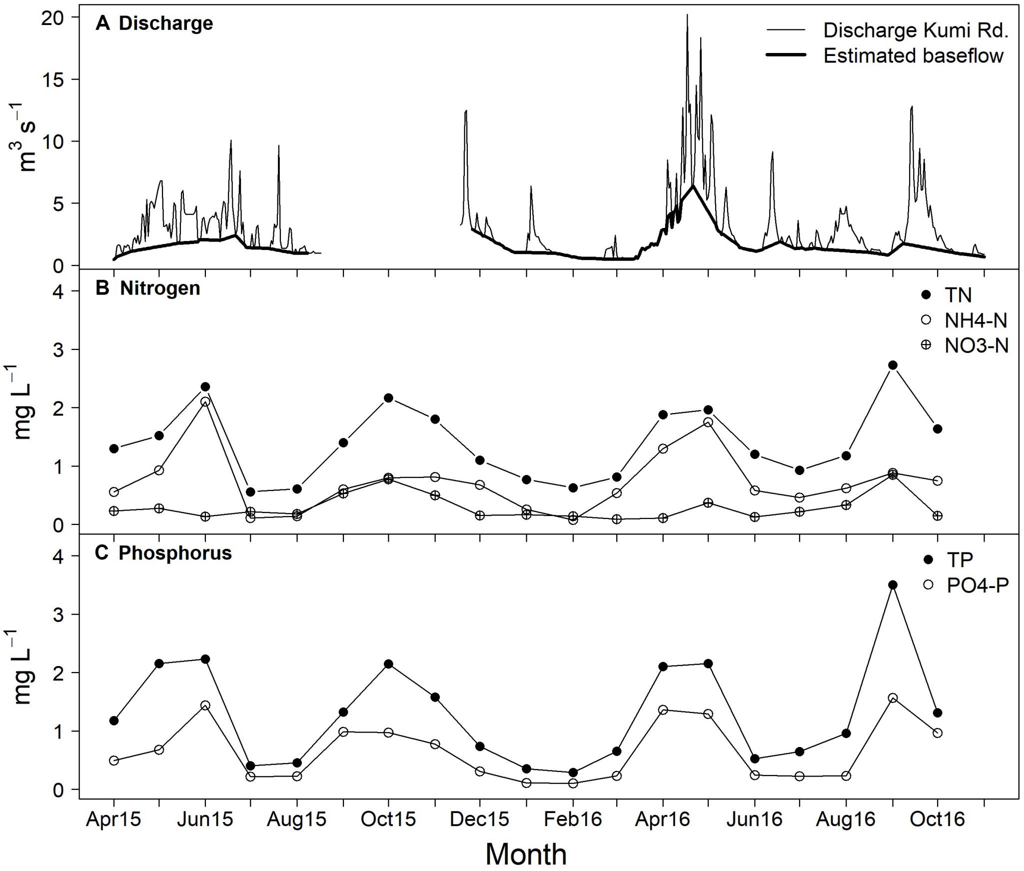

FIGURE 6 | (A) Separation of baseflow for the Namatala River; **(B)** nitrogen concentration; and **(C)** phosphorus concentration; all at Kumi Road, Mbale, during the experimental period. Daily discharge data from the gauge at Kumi Road were used from the period 2000–2015 using the method from WMO (2008). Estimated Base Flow Index (BFI) for Namatala River was 0.605. Owing to a technical problem at the gauging station, there was a gap in discharge data in the period August–November 2015. For further explanation, see text.

and health risks, especially if they also carry high amounts of heavy metals or other contaminants (K'oreje et al., 2016; Sereyrath et al., 2016). With a growing urban population, the load from these streams may increase in the future. On the other hand, the riparian communities also utilize these nutrient-rich streams to cultivate maize and vegetables (Namaalwa, pers. obs.).

Compared with the polluted urban streams, the rice farming in HGMU 3 had a much stronger effect on sediment and nutrient concentrations and loads entering the river. Significantly higher sediment and nutrient concentrations and EC were observed in Naboa, downstream of HGMU 3, compared with sampling points upstream and downstream of Naboa. Also, DO concentration decreased significantly between Jami and Naboa, and concentrations of TN, TP, and TSS within HGMU 3 were significantly higher than in the other HGMUs. These high nutrient and sediment concentrations likely originate from the commercial rice farming in HGMU 3, which involves a high degree of tillage erosion and drainage that lead to elevated concentrations of TSS, accompanied by NH_4-N and PO_4-P that are known to adsorb to soil particles (Shore et al., 2015; Weigelhofer et al., 2018). Leaching from agricultural soil can also lead to the increase in EC and the lower DO concentrations at Naboa. It is also likely that fertilizers are applied in these rice farms, although interviews with farmers reported no use of fertilizers (Namaalwa, unpublished results). This can be expected to increase NH_4-N and PO_4-P concentrations from mineralization under the prevailing high temperatures, slightly alkaline pH and the alternate soil drying and wetting between seasons (Manguiat et al., 1996; Sahrawat, 2010).

The combination of land use in the wider catchment and agricultural practices within the wetland provide a complex seasonal dynamic, leading to loss of the retention function in the agricultural zones of Namatala Wetland. Increased discharge during the months of greater precipitation (March-June; Sept-November) increased the nutrient concentrations and loads from all surface inflows. Farming practices in HGMU 1 have permanently changed the ecological character of this area, which is now mostly disconnected from the river. Similar long term changes to surface water flow patterns caused by agriculture have been reported in headwater catchments in western Kenya (Recha et al., 2012). Plowing (between January and March) and weeding (in April and October) take place just before the onset of the

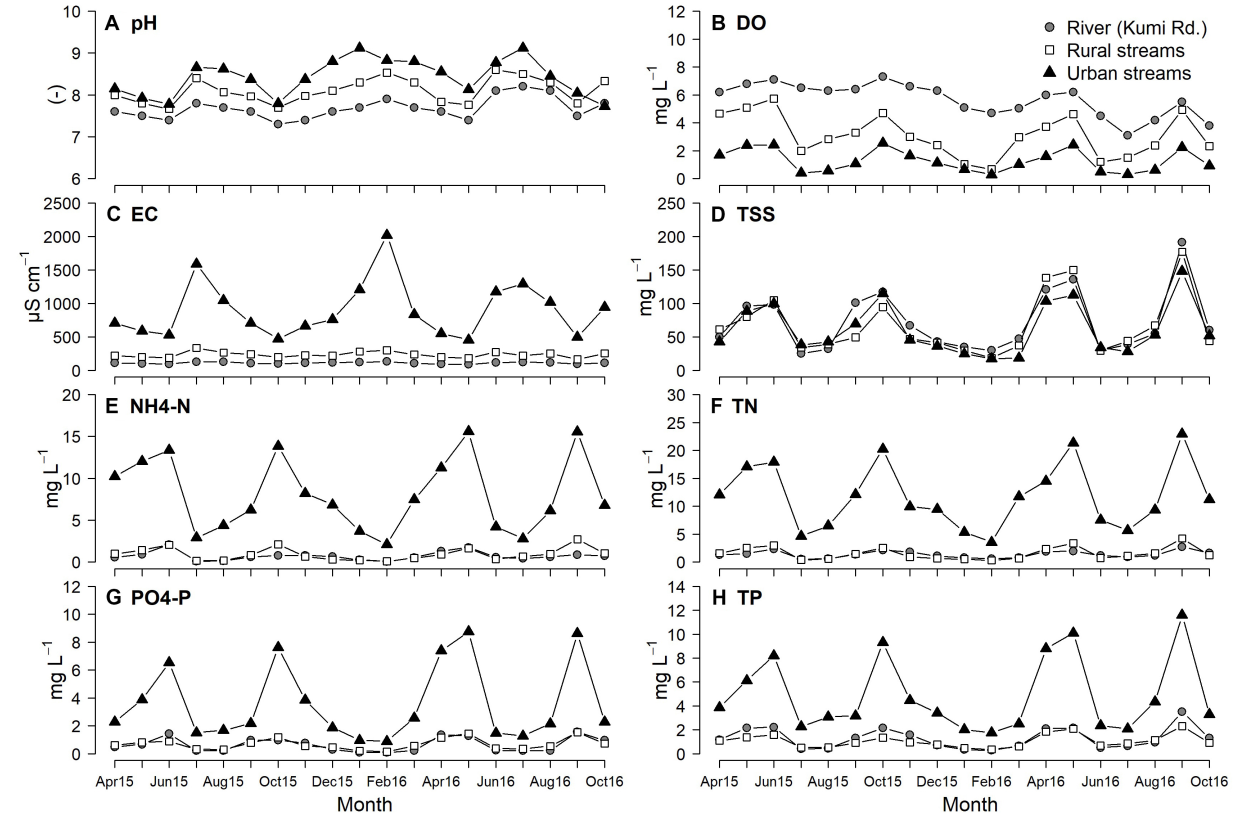

FIGURE 7 | Variation of water quality parameters in Namatala River (at the Kumi Road sampling point), urban streams (mean value of four streams) and rural streams (mean value of three streams) of Namatala Wetland, Uganda, in the period April 2015–October 2016. **(A)** pH; **(B)** dissolved oxygen (DO); **(C)** electrical conductivity (EC); **(D)** total suspended solids (TSS); **(E)** ammonium nitrogen (NH_4-N); **(F)** total nitrogen (TN); **(G)** soluble reactive phosphorus (PO_4-P); **(H)** total phosphorus (TP).

rainy season, increasing sediment suspension and the release of sediment-bound nutrients into the water column. This results in a pulse of sediment and nutrients that is carried downstream. The modified agricultural zones (HGMUs 1 and 3) cannot retain this pulse. A similar synchronicity of seasonal rainfall and agricultural practices was observed in the Migina catchment in Rwanda (Uwimana et al., 2018).

Downstream of Naboa in HGMUs 4 and 5, sediment and nutrient concentrations in the river gradually decreased. Values in Irabi, the most downstream sampling point, were lower than those at the Kumi Road station. Here discharge was also much lower and, as the river connects laterally with the wetland, the water quality is typical of papyrus wetlands found elsewhere (Kansiime et al., 2007; van Dam et al., 2014). DO concentrations in these wetlands are low because of accumulation of organic matter from decaying vegetation, and pH decreases from accumulation of humic acids Whereas the decrease in DO concentration in the river after HGMU 3 can be seen as a negative impact of farming activities, the low DO in HGMUs 4 and 5 is partly a natural feature of the papyrus wetland.

The yield calculations show that HGMUs 4 and 5 retain sediment and nutrients, whereas HGMU 3 exports them. The net yields calculated for each HGMU can be interpreted as the retention of sediment or nutrients within that area. Because of the location of the sampling stations, it was not possible to calculate net yield for HGMU 2, and the calculations for the other HGMUs should be seen as crude indications for sediment and nutrient retention. Nevertheless, there were clear differences in net yield with HGMUs 4 and 5, showing mostly positive net yields throughout the year, while HGMU 3 generally had negative net yields. HGMU 1 had net yields close to 0. The significant regressions of net yield with discharge show that retention increased with higher discharge in HGMUs 4 and 5, while it decreased in HGMU 3. The positive slopes of these regressions in HGMUs 4 and 5 were all greater (about double for TSS and TP, and almost triple for TN) than the negative slopes in HGMU3, suggesting that retention capacity of the two downstream HGMUs still compensated for the increased export of sediment and nutrients from HGMU 3 during period with high discharge.

The retention function of the lower Namatala Wetland is likely the result of the intact lateral connectivity with the river, with high flows dispersing and slowing down in the downstream zone of the wetland, where there is ample opportunity for sedimentation, adsorption and uptake. Sediment and nutrient retention in floodplains and buffer zones are influenced by many factors, including length of the inundation period, hydraulic characteristics of the soil,

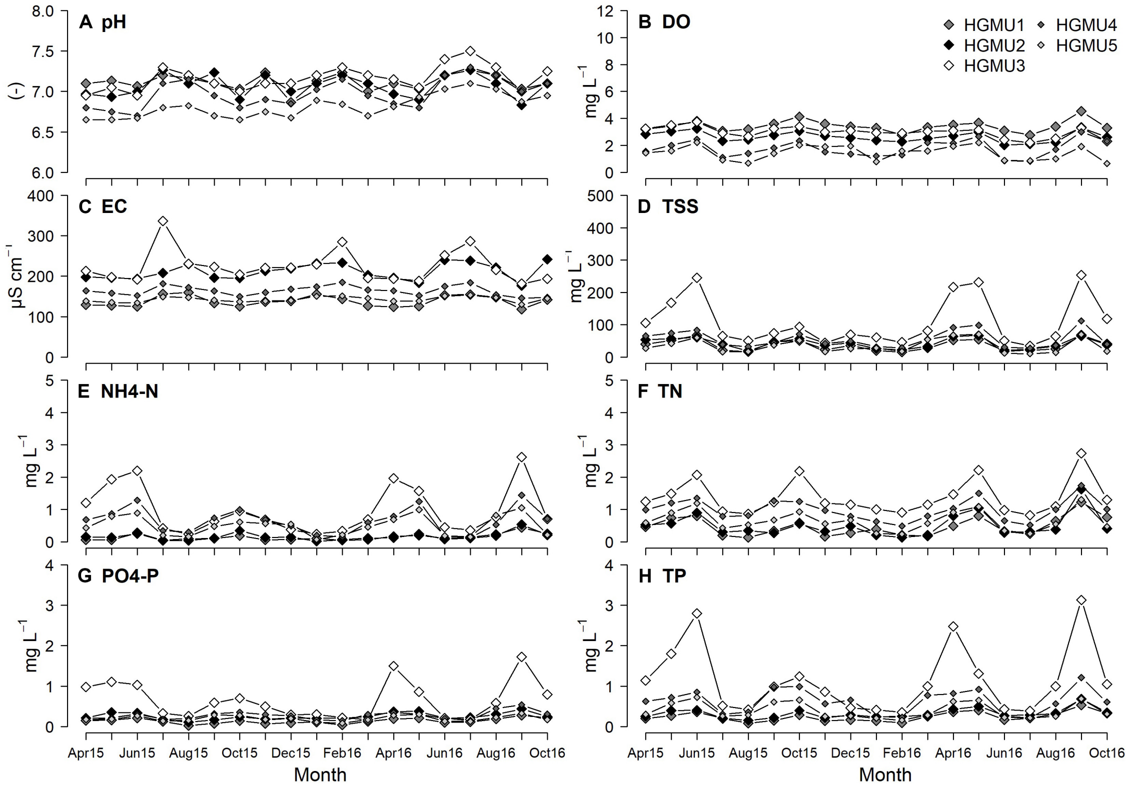

FIGURE 8 | Seasonal variation of water quality parameters in HGMUs 1–5 of Namatala Wetland, for the period April 2015–October 2016. **(A)** pH; **(B)** dissolved oxygen (DO); **(C)** electrical conductivity (EC); **(D)** total suspended solids (TSS); **(E)** ammonium nitrogen (NH4-N); **(F)** total nitrogen (TN); **(G)** soluble reactive phosphorus (PO_4-P); **(H)** total phosphorus (TP).

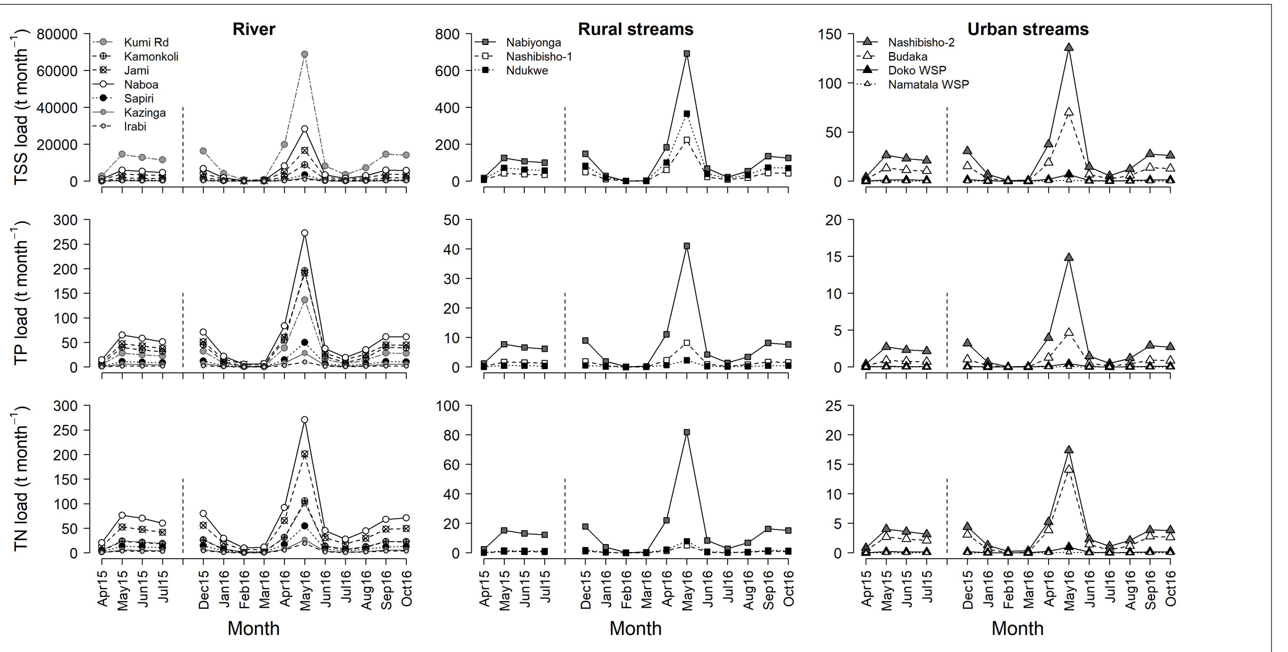

FIGURE 9 | Total suspended solids (TSS), total phosphorus (TP), and total nitrogen (TN) loads (tonnes month^{-1}) from the different streams of Namatala Wetland in the period April 2015–October 2016. For details of load calculations, see text. Loads between August and November 2015 could not be calculated because discharge data from the Kumi Road gauging station were not available.

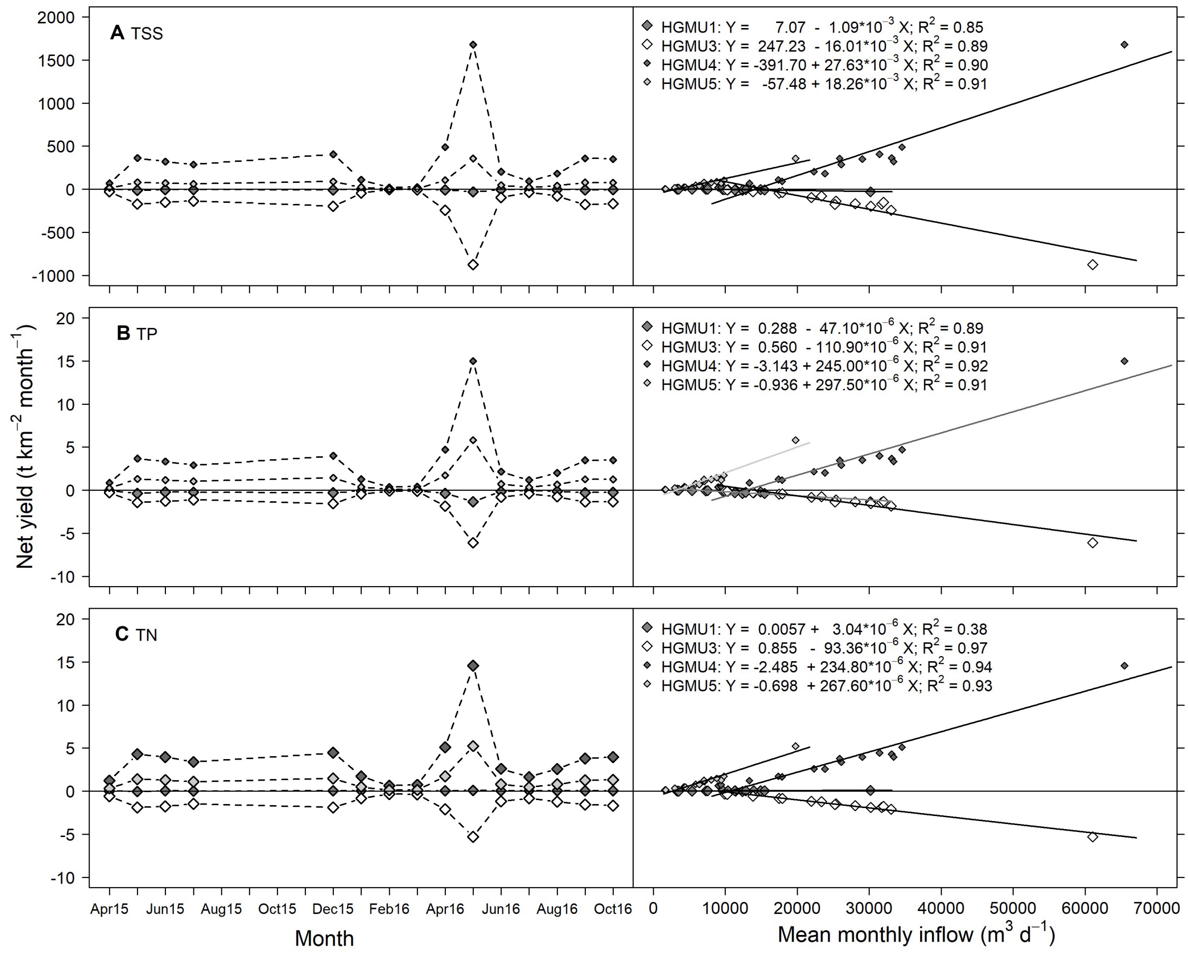

FIGURE 10 | Net yield (tonnes km^{-2} month^{-1}) (left panel), and regression of net yield (Y) on mean monthly inflow (X) (right panel). **(A)** Total suspended solids (TSS); **(B)** Total phosphorus (TP); **(C)** Total nitrogen (TN). Data are from the period April 2015–October 2016 in HGMUs 1, 3, 4, and 5 of Namatala Wetland. For further explanation, see text.

relative contributions of groundwater and surface water, and characteristics of vegetation and microbial communities (Noe and Hupp, 2007; Weigelhofer et al., 2018). The retention of phosphorus is strongly linked to sedimentation of particulate matter (Shore et al., 2015), and in papyrus wetlands adsorption of phosphorus to sediment can be important (Kelderman et al., 2007). For nitrogen, sub-surface transport and nitrification-denitrification are generally more important pathways (Pärn et al., 2012; Weigelhofer et al., 2018) although in Namatala Wetland, NH_4-N adsorption to sediment may also play a role. In headwater streams, nitrification of NH_4-N and uptake of NO_3-N by benthic periphyton dominate N removal (Peterson et al., 2001). In more downstream river reaches impacted by agriculture, the relative importance of coupled nitrification-denitrification is, however, likely reduced (Kemp and Dodds, 2002). In Namatala Wetland, most of the TN consisted of NH_4-N, which is more likely to be taken up by the papyrus vegetation and accumulate in peat than to be removed by nitrification (Hes and van Dam, 2019). Nevertheless, NO_3-N concentrations also decreased toward the downstream stations. Partly this could reflect uptake by biota in the wetlands, but the conditions for denitrification are good with low DO and high organic matter availability. Experiments on potential denitrification in Namatala Wetland showed much higher potential in the intact wetland zones than in agriculturally converted soils (Namaalwa et al., unpublished results).

Results from this study demonstrate that the Namatala Wetland delivers important regulating ecosystem services for the downstream Mpologoma River and the Lake Kyoga catchment. However, this function of the wetlands is at risk. The connectivity and integrity of the downstream wetland zone are threatened by encroachment and further development of agriculture, accompanied by overharvesting and removal of papyrus. Similar developments have been observed in the East African region (Maclean et al., 2013; Bateganya et al., 2015; Uwimana et al., 2018). Future management strategies of Namatala Wetland should include sustainable agriculture in the upper wetland, including introduction of buffer strips along the main river channel, conservation of the remaining papyrus swamp and its connectivity with the river in the lower wetland, and improved wastewater treatment (including integrated nutrient management) around Mbale town. Options for reducing erosion and nutrient runoff caused by rice farming in HGMU 3 should be considered. Support among stakeholders for integrated management solutions and more sustainable farming practices seems to be present (Zsuffa et al., 2014) and can be used, together with the results of this study, to strengthen wetland management planning for Namatala Wetland and similar wetlands in Uganda.

Land use change has a strong impact on landscape sediment and nutrient retention (Burt and Pinay, 2005; Jung et al., 2008; Uwimana et al., 2018). This study shows that the agricultural and urban development pressure in the upstream zones of the wetland can be mitigated to a large extent by the natural functioning of the downstream zones of the wetland ecosystem. This delicate balance between economic development and wetland protection is representative of many wetlands in Africa and other parts of the world, and determining a sustainable level of wetland use is a challenge for many wetland managers and governments (Ramsar Convention on Wetlands, 2018). Detailed knowledge of water and nutrient flows in relation to natural variation, local conditions and land use is important, but more studies on rivers and wetlands in Africa are needed. Besides water quality regulation, other ecosystem services such as fish production, tourism, and biodiversity conservation should be taken into account. Practical methods for quantifying different ecosystem services and determining optimum management strategies are needed (Wood et al., 2013; Zsuffa et al., 2014). A lot of useful information could be obtained from regular monitoring of hydrology and water quality, but this is often lacking. Economic valuation studies show that the monetary value of water quality regulation by wetlands often exceeds the value of the provisioning services (Emerton et al., 1999; Russi et al., 2013). Allowing agricultural and urban development to gradually replace natural wetlands is, therefore, also economically undesirable. Lost regulating services need to be replaced through capital investment in water treatment facilities.

CONCLUSION

Urban streams had significantly higher concentrations of sediment and nutrients than the Namatala River and its tributaries. However, the largest loads of sediment and nutrients were carried into the wetland by the Namatala River. The largest nutrient loads were observed downstream of the main rice growing area in the central part of the wetland. Sediment and nutrient loads were strongly related to seasonal variation in rainfall and river discharge, and to the corresponding peaks in agricultural practices. Peak loads coincided with the rainy seasons and consisted of accumulated material from densely populated urban areas, as well as sediment and nutrients from intensively cultivated parts of the wetland. The capacity for sediment and nutrient retention was 2–3 times higher in the downstream part of the wetland with more intact papyrus vegetation and lateral hydrological connectivity. Retention in the downstream part of the wetland increased at higher river flow rates. On balance, the sediment and nutrient retention in the intact parts of Namatala Wetland absorbed the export from the converted parts. It can be concluded that Namatala Wetland still performs its sediment and nutrient regulating ecosystem services in the Lake Kyoga catchment. However, further conversion to agriculture puts this function of the wetland at risk. To maintain the regulating ecosystem services of Namatala Wetland in the future, improved wastewater treatment, sustainable agricultural practices and conservation of the remaining intact wetland zone are needed. Detailed knowledge of the sediment and nutrient retention processes can be used for determining trade-offs in sustainable wetland management.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request from the corresponding author.

AUTHOR CONTRIBUTIONS

SN designed the research, performed field and laboratory measurements, and took the lead in writing the manuscript. AD and GG contributed to research design, data analysis, and manuscript editing. IZ advised on the hydrological aspects and contributed the hydrograph separation analysis. All co-authors provided research guidance and critical reviews of the manuscript.

FUNDING

This study was funded by the EU-FP7 WETwin project (project no. 212300), the Netherlands Fellowship Programme (NFP) through Nuffic (grant no. CF9174/2013), and the International Foundation for Science (IFS Sweden, individual grant no. W5416).

ACKNOWLEDGMENTS

We would like to thank the Directorate of Water Resources Management (DWRM), Entebbe, Uganda, for the river discharge, water level and rainfall data. Special appreciation is expressed to the NWSC Central Laboratory Bugolobi for the space and laboratory equipment provided during the research. Special thanks to the field assistants Bright Twesigye, Robert Katungi, and Aloysius Bukenya.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00148/full#supplementary-material

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Conflict of Interest: IZ was employed by VITUKI Hungary Plc., Budapest, in addition to his affiliation to National University of Public Service, Budapest Hungary.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
published: 07 December 2020
doi: 10.3389/fenvs.2020.502042

Protected Areas and Endemic Freshwater Fishes of the Cape Fold Ecoregion: Missing the Boat for Fish Conservation?

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Edited by:
Rebecca Elizabeth Tharme,
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Reviewed by:
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University of Mpumalanga,
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Specialty section:
This article was submitted to
Freshwater Science,
a section of the journal
Frontiers in Environmental Science

Received: *01 October 2019*
Accepted: *13 November 2020*
Published: *07 December 2020*

Citation:
Jordaan MS, Chakona A and van der Colff D (2020) Protected Areas and Endemic Freshwater Fishes of the Cape Fold Ecoregion: Missing the Boat for Fish Conservation? Front. Environ. Sci. 8:502042. doi: 10.3389/fenvs.2020.502042

Freshwater systems and their associated biodiversity are among the most threatened ecosystems globally. The greatest threats to freshwater fishes are the introduction and spread of non-native species, pollution, habitat degradation and loss, and overexploitation. While many regions across the world contain extensive networks of protected areas, these are largely ineffective for protecting riverine systems and their biodiversity. This is because they were designed with the aim of prioritising conservation of terrestrial biodiversity, with limited or no consideration for aquatic systems. The Cape Fold Ecoregion, located within the Western and Eastern Cape Provinces of South Africa, is home to the highest percentage of threatened freshwater fishes in the country. The region has an extensive protected area network that protects a wide array of ecosystems, but limited information exists on the role of protected areas in conserving the endemic freshwater fish fauna of this region. This study evaluated the value of protected areas for protection of freshwater fishes in the Western Cape Province by setting species conservation targets and then intersecting species distribution data with protected area polygons. Conservation targets were set to protect the minimum viable population required for long-term persistence, with a minimum of 10 subpopulations as a target. This, along with other factors such as population viability and protected area effectiveness was used to determine whether a species was effectively protected by the current protected area network. Species were classified into one of four categories; (1) "well protected," (2) "moderately protected," (3) "poorly protected," and (4) "not protected." Our results indicate that the majority of native fishes are inadequately protected within the current protected area network in the province. This is mainly a result of the linear nature of riverine ecosystems that exposes them to impacts and threats that emanate from outside of the protected area. These limitations are not unique to the CFE, and our findings have broader implications as they highlight the need for integrating both the riverine and terrestrial ecosystems in the design, expansion and management of protected areas. This will enhance and maximise conservation and protection of riverine systems and their unique biodiversity.

Keywords: Cape Fold Ecoregion, freshwater fish, biodiversity, protected area effectiveness, invasive fish, conservation interventions

INTRODUCTION

Freshwater fishes are one of the most imperilled vertebrate groups globally (Reid et al., 2013). The introduction and spread of non-native species, pollution, habitat degradation and loss, hydrological modifications, construction of instream barriers, excessive water abstraction, overexploitation and intensification of agricultural activities have been identified as the key threats to freshwater ecosystems and their biodiversity (Ricciardi and Rasmussen, 1999; Collares-Pereira and Cowx, 2004; Dudgeon et al., 2006; Darwall et al., 2011; Laurance et al., 2014). Because of these multiple impacts and threats, freshwater ecosystems continue to receive increasing global attention in a quest to determine effective ways to mitigate against the projected mass extinction of freshwater fishes (Ricciardi and Rasmussen, 1999; Azevedo-Santos et al., 2019). Although many regions across the world contain extensive networks of protected areas, their effectiveness in protecting riverine systems and their biodiversity has been increasingly questioned over recent years. This is because historically the designation of protected areas was largely informed by the need to protect terrestrial biodiversity (Thieme et al., 2012; Juffe-Bignoli et al., 2016; Azevedo-Santos et al., 2019). Despite being ranked as the most highly threatened ecosystems globally, freshwater systems have been overlooked in the designation of protected areas, and often, their inclusion in current protected areas has mainly been coincidental rather than intentional (Abell et al., 2011). The lack of integration of freshwater systems in protected area designation and establishment has been identified as the main reason for their limited efficacy in protecting freshwater fishes, for example large migratory fishes that require large areas to complete their life cycles are considered to be poorly protected in Brazil (Azevedo-Santos et al., 2019). Similarly, Chessman (2013) reported that protected areas offered no real benefit to the native fish in the Murray–Darling Basin of Australia, because they did not effectively mitigate threats related to non-native fish and alteration of water regimes. Lawrence et al. (2011) reported that while nearly two-thirds of native fishes occur in national parks in the United States, only 18% of highly imperilled fish species are represented within protected areas.

In a systematic evidence review of case studies of protected areas and freshwater biodiversity, Acreman et al. (2019) reported that just over half of these areas had positive outcomes for freshwater biodiversity. Reasons for reduced effectiveness include inadequate connectivity within freshwater ecosystems, lack of protection for migratory species beyond designated areas, limited control over threats from outside the protected area and the absence of a whole catchment approach (Acreman et al., 2019). From this, it is evident that the degree of protection for riverine ecosystems is largely dependent on the location of the protected area within the landscape. This is because the linear nature of riverine ecosystems exposes them to impacts and disturbances that occur outside the protected area and can be transmitted downstream from the point of impact for distances proportional to the scale and nature of the disturbance (Davies et al., 1993; Skelton et al., 1995). Protected areas located in headwater sections of catchments are also only likely to be effective in protecting a limited number of fish species that are associated with mountain streams, but will provide no protection to taxa in the lower sections of rivers with gentle gradients where there is increased intensity of human activities. Rivers are also inextricably linked to their catchments, and as such, some disturbances that may occur outside the protected area (for example introduction of non-native species) could spread and impact the whole catchment, including sections in the protected area (Wilkinson et al., 2018). The effectiveness of a protected area is therefore strongly determined by the extent of the catchment included within the protected area, as well as location and configuration of the reserve with respect to the catchment area (Skelton et al., 1995; Saunders et al., 2002; Collares-Pereira and Cowx, 2004; Juffe-Bignoli et al., 2016). For reserves located in headwater sections of rivers, instream barriers located in the lower sections can prevent upstream invasion and establishment of non-native fish species (Fausch et al., 2009; Ellender et al., 2011).

In southern Africa, the highest concentration of threatened freshwater fish is found in the Cape Fold Ecoregion (CFE) located at the southern tip of the continent, where more than 50% of the endemic fish fauna are listed in highly threatened categories of the IUCN as Critically Endangered (11%), Endangered (33%), and Vulnerable (11%). Indeed, evidence from previous and ongoing studies indicate that the number of threatened species in the CFE remains severely underestimated. Some of the species that are currently listed as Data Deficient or Least Concern, for example Cape kurper *Sandelia capensis*, Cape galaxias *Galaxias zebratus*, and chubbyhead barb *Enteromius anoplus* are complexes of several narrow range endemic lineages, some of which are likely to represent distinct species (Chakona et al., 2013; Bronaugh et al., 2020). Non-native piscivores and habitat degradation are ranked as the greatest threats to freshwater fishes of the CFE (Tweddle et al., 2009; Ellender and Weyl, 2014). A total of 15 introduced species have become established in the CFE, with some, such as common carp *Cyprinus carpio*, rainbow trout *Oncorhynchus mykiss*, basses (*Micropterus spp.*), and bluegill sunfish *Lepomis macrochirus* having widespread distributions that extend into rivers in formally protected areas (Jordaan et al., 2012). These species affect native species through predation, habitat alteration, competition for resources, the introduction of diseases and the disruption of ecological processes (De Moor and Bruton, 1988; Ellender and Weyl, 2014). The primary impact is predation and this has resulted in the extirpation of most native species from mainstream rivers and many tributaries within the CFE (Weyl et al., 2014; Van der Walt et al., 2016). Remnant populations of native species are now limited to upper reaches of tributaries above waterfalls and other barriers that prevent range expansion of non-native species (Skelton, 2001; Chakona et al., 2013, 2020).

While multiple anthropogenic impacts have transformed much of the landscape and riverscapes in the CFE, the region also has a comprehensive network of formally protected areas declared under the National Environmental Management: Protected Areas Act (Act 57 of 2003). These protected areas are essential tools for the conservation of biodiversity and prevent land-use practices that could impact ecosystem integrity (Gray et al., 2016). As with many other parts of the world, the current protected area network in the region is mostly a result of opportunistic reservations over time. In the past, there was limited formal conservation planning to ensure representation of both the patterns (taxa and land classes) and processes that underpin the persistence of biodiversity (DEA, 2016). Within the CFE, for example, establishment of protected areas almost exclusively focused on the protection of terrestrial ecosystems, especially endemic vegetation types (Wicht, 1945; Rebelo, 1997; van Wilgen et al., 2016). In recent years (since 2008), South Africa has invested in a National Protected Area Expansion Strategy (NPAES) to address this shortfall (DEA, 2016). Other areas that were also afforded protection included economically marginal regions that were less suitable for agricultural development or human habitation and where reservation costs were low (Rebelo, 1997). In the CFE, this resulted in a protected area network that predominantly comprises rugged, high altitude mountain areas, whereas the economically productive lowland areas have been heavily transformed through various land-use activities (Rouget et al., 2003b).

There is growing realisation that the existing protected area network is inadequate for conserving both aquatic and terrestrial biodiversity in South Africa, as for example, more than 30% of river types and 25% of vegetation types are not represented within conservation areas in the country (Rebelo, 1997; Nel et al., 2009). This prompted the need for expansion of protected areas, but there are concerns that these actions may not achieve the desired conservation outcomes as expansions are likely to be biased towards focusing on areas adjacent to existing protected (mainly high altitude) areas to facilitate management (Rouget et al., 2003a). This is a significant cause for concern given the ongoing and increasing levels of land transformation and loss of biodiversity in lowland areas (Rouget et al., 2003a; van Wilgen et al., 2016).

In light of the ongoing and projected threats to the endemic freshwater fish fauna of the CFE (Ellender et al., 2017; Shelton et al., 2018), there is need for an assessment of the effectiveness of the current network of protected areas in mitigating these threats. Although previous studies have documented the distribution and conservation status of freshwater fishes in protected areas in the country and the region (Skelton et al., 1995; Impson et al., 2002; Russell, 2011), these studies did not evaluate long-term persistence. This requires some consideration for whether the population within the protected area is viable and what the minimum number of these populations are for persistence of the species into the future. The recent discovery of hidden diversity and description of new species within a number of fish genera in the CFE (e.g., Chakona et al., 2013) also necessitated the need to update information on species distribution ranges and evaluate the degree of protection afforded to them by formally protected areas. The aim of the present study was thus 2-fold: (i) to provide an updated inventory of species distributions in protected areas that reflect the latest taxonomic information and, (ii) to assess the effectiveness of the current protected area network in conserving native freshwater fishes of the CFE. Given that these protected areas were designated for protection of unique plant diversity, particularly in high altitude areas, it was predicted that headwater species would be better protected than lowland species.

MATERIALS AND METHODS

Input Data

Only native primary freshwater fishes were included in this assessment and both obligate and facultative catadromous species were excluded from the assessment. Other species excluded were those of marine origin that can complete their life cycle in freshwater such as the river goby *Glossogobius calidus*. Also excluded were estuarine and marine species that enter freshwater systems but do not maintain permanent breeding populations in these rivers such as moonies (*Monodactylus* spp.). Extra-limital populations of native fish species were not included in the assessment irrespective of the conservation status of that species and only populations within the native range of the species were considered. Data Deficient species were excluded from this assessment due to paucity of distribution data or as a result of taxonomic uncertainty.

For the taxa included in the assessment, specimen-linked point distribution data were obtained from the South African Institute for Aquatic Biodiversity (SAIAB, 2016) for each of the 31 taxa assessed. This dataset formed the basis of the 2016 Red List Assessment (RLA) of the freshwater fishes of South Africa (SANBI, 2016). Prior to the current study and the RLA, all distribution data were verified by taxon specialists and updated where relevant to ensure that all recently collected data were included and any data points based on possible misidentification of species were excluded. The cleaned distribution data were intersected with a polygon shapefile of South Africa's protected area network (Government of South Africa, 2010) using ArcGIS software (Version 10). Protected areas recognised in terms of the South African National Environmental Management: Protected Areas Act (Act 57 of 2003) and considered secure into the future were included (Forest Wilderness Areas, Forest Nature Reserves, World Heritage Sites, Wilderness Areas, Provincial Nature Reserves, Mountain Catchment Areas and National Parks). This intersected data produced a list of protected areas for each species. To ensure that no species was excluded from a protected due to differences in point data precision, after intersecting the data, the inferred presence was determined by examining the points near the boundary of the protected area (≤1 km). Expert knowledge was used to infer the presence of these species in a protected area, based on their knowledge of the species ecology and whether suitable habitat was available inside the protected area. For future iterations of this analysis, these points should be ground-truthed. Further, when a protected area had multiple geographically isolated sections, these were assessed as individual protected areas and recorded individually (**Supplementary Appendix 1**).

As non-native invasive fishes are considered a primary threat to a large number of native freshwater fish taxa in Southern Africa (Tweddle et al., 2009), their presence on a protected area was one of the primary drivers affecting the scoring of the effectiveness of the protected area. This required additional input data on alien fish distributions and instream invasion barriers. The primary sources of this information was unpublished survey data and expert knowledge, supplemented with peer reviewed literature where available. While impacts associated with changes in water quality and quantity are also an important threat to freshwater fishes, available data was too limited for inclusion in the assessment.

Assessment Methodology

Pfab et al. (2011) provided conservation targets for species persistence and the minimal number of subpopulations that are needed to ensure survival into the future. Ideally, conservation targets can be set in terms of a minimum viable population size of 10, 000 individuals or 10 viable subpopulations per species, supported by IUCN RLA criteria (IUCN 2001) and as proposed by Pfab et al. (2011), respectively. However, there is limited population density or abundance data available for the majority of freshwater fishes of the region. In this study, conservation targets could only be set in terms of the number of viable subpopulations and not actual population sizes. Subpopulation viability was determined based on information included in the latest RLAs. All subpopulations on protected areas were scored as either viable or not viable with default values of 1,000 or 100 individuals assigned, respectively (**Supplementary Appendix 2**). In the case of more than one population of a species present in the same protected area, the viability and protection level was assessed at the individual subpopulation level and not at the protected area level.

Furthermore, in the case of naturally range-restricted or rare species, allowances were made for adjustments in the conservation target to be less than 10 viable subpopulations (representing a target of 10,000 individuals). An example of this would be Barnard's rock catfish *Austroglanis barnardi* which is naturally range-restricted and warranted a reduced conservation target of five viable subpopulations (representing a target of 5,000 individuals). When such adjustments were made, it was motivated and open to review from other freshwater fish experts. In future iterations of this analysis, a review process for such adjustments is recommended. In cases where species were lost from large sections of their natural distribution range due to threats, conservation targets were not adjusted.

In addition to determining species representation within protected areas, the effectiveness of the protected area in safeguarding the species was also assessed. A default value of one was assigned in the case of a protected area being highly effective in protecting the species against major threats and ensuring the long-term persistence of the population present within the protected area. Default values of 0.5 and 0.1 were assigned to "fair" and "poor" levels of protection afforded by the protected area, where the protected area was either moderately effective in mitigating some of the threat to the species (0.5) or completely ineffective in mitigating the major threats (0.1). Given that non-native invasive fishes, especially *Micropterus* spp. and *O. mykiss* are considered the primary threat to the majority of native Southern African freshwater fishes, any river within a protected area where these species have become established were given a poor protection score. This was irrespective of other variables such as habitat availability and water quality within the protected area. As many invasions occur from mainstream or downstream sources, only rivers where the headwaters are fully within the protected area and where known invasion barriers exist were rated as having a fully effective protection function for the species in question. Other threats were scored based on available data and expert knowledge of the protected area.

In summary, the protection category was assigned based on the number of individuals protected (a function of the number of populations on protected areas as a function of their viability and protection effectiveness), relative to the conservation target (set as 10,000 individuals unless stated otherwise). This methodology is presented in detail in **Supplementary Appendix 2**. Protection categories were: "not protected": <5% of the conservation target met within protected areas; "poorly protected": 5–49% of the conservation target met within protected areas; "moderately protected": 50–99% of the conservation target met within protected areas; "well protected": 100% + of the conservation target met within protected areas. These categories follow from well-established and accepted ecosystem categories for South African ecosystem protection level assessments (Driver et al., 2012). It must be noted that a constraint to effectively assessing all CFE fish species in terms of protection was variation in data quality and quantity and to address this, a confidence score (high, medium, or low) was awarded to each assessment.

RESULTS

Of the 45 known freshwater fish taxa in the CFE, 31 were assessed using the described methodology. Species native to the CFE but excluded from the current assessment due to either taxonomic uncertainty or limited distribution data were *E. anoplus, Enteromius pallidus, G. zebratus,* and *S. capensis*. The moggel *Labeo umbratus* was also excluded as it has a wide distribution range outside the CFE. For assessed taxa, a conservation target of 10 000 individuals were set with the exception of the Tradouw redfin *Pseudobarbus* sp. nov. "Tradouw," Krom River redfin *Pseudobarbus senticeps,* Twee River redfin *Sedercypris erubescens,* Doring River redfin *Pseudobarbus* sp. nov. "Doring," *Galaxias* sp. nov. "Goukou" and Barnard's rock catfish *Austroglanis* *barnardi* (**Table 1**). These taxa are all highly range-restricted and a conservation target of 10,000 individuals were considered unrealistic. The conservation target was reduced to 5,000 individuals based on natural low abundance or restricted natural distribution ranges. It was found that 112 out of the 163 (67%) populations assessed was done with high confidence. Populations with low confidence scores were sites where recent survey data were not available and thus assessors relied on expert knowledge of the past conditions of those areas to score population viability and protected area effectiveness. Only eight (5%) populations received a low score, highlighting the need for surveys in these protected areas.

Results indicated that 21 of the 31 taxa (68%) are either "poorly protected" (39%), "not protected" (10%) or are absent from any form of formally protected area (19%). These categories indicate that less than 49% of the conservation target for these taxa are being met within the current protected area network. For the remaining 10 taxa that were assessed, five (16%) were "moderately protected" with an additional five (16%) considered "well protected" (**Table 1** and **Figure 1**). In terms of presence on formally protected areas, 11 taxa (35%) occurred on 1–3 protected areas with an additional seven taxa (23%) present on 4–8 protected areas. Three taxa (10%) was recorded from 9 to 12 protected areas with 2 species (6%) present on 13–18 protected areas and a further two being present on >18 formally protected areas (**Figure 2**).

When considering protection level relative to conservation status, it is evident that the majority of taxa in the "no intersect" to "poorly protected" categories comprise Critically Endangered (CR) and Endangered (EN) taxa (**Figure 3**). The only Vulnerable (VU) taxa in these categories are two Galaxias lineages *Galaxias* sp. nov. "Gouritz" and *Galaxias* sp. nov. "Goukou," both of which are listed under category D2 for small and restricted populations that are at high risk from future threats. The only Near Threatened (NT) species listed in the "poorly protected" category is the Clanwilliam sawfin *Cheilobarbus serra* but it must be noted that this species is close to meeting the criteria for being "moderately protected" as 45% of the conservation target is being met within formally protected areas (**Table 1**). For the category of "moderately protected" one taxon is listed as CR, two as EN and one each as VU and NT respectively. Of the five taxa that were assessed as "well protected" four are listed as NT with one taxon listed as VU (**Figure 3**).

When excluding protected area effectiveness from the analysis and only considering the number of viable populations within a protected area, all species improved in terms of the percentage of the conservation target met within protected areas and 12 species changed protection category (**Table 1** and **Figure 4**). Three species changed status from "not protected" to "poorly protected." These species had one to two populations within a protected area, however these populations were severely impacted by non-native fish species as the protected areas did not provide any mitigation against this threat. Six species changed from "poorly protected" to "moderately protected" and three moved from "moderately" to "well protected." When considering reduced protected areas effectiveness, the primary driver was the presence of non-native fish species within the protected area and the lack of control measures. Secondly, impacts associated with poor land-use practices occurring outside the boundaries of the protected area also served to reduce the effectiveness of the protected area.

DISCUSSION

Based on available distribution data and using the methodology that considers both species presence and protected area effectiveness, there is evidence that the current protected area network within the CFE is inadequate for the protection of many freshwater fish taxa of the region. Alarmingly, 84% of taxa are under-protected (16% "moderately protected," 39% "poorly protected," 10% "not protected," and 19% are completely absent from formally protected areas). Only 16% of taxa can be regarded as "well protected," indicating that 100% or more of the conservation target is being met within formally protected areas. This is in contrast to Impson et al. (2002) who reported the freshwater fishes of the CFE, including threatened taxa, to be "well protected," as only two of the 19 known taxa were not recorded in protected areas. These apparently conflicting results must however be interpreted with caution and can be explained with three arguments. Firstly, there has been major taxonomic revisions in the past decade, resulting in a different compliment of species included in the present assessment to those assessed by Impson et al. (2002). Secondly, while the former study considered national parks, provincial nature reserves and local authority nature reserves, the present study included all areas declared under the National Environmental Management: Protected Areas Act and thus assessed additional areas such as mountain catchment areas and stewardship areas. Finally, while Impson et al. (2002) only reported presence of native species in protected areas, the present study quantified the number of populations per area and evaluated the population viability as well as the effectiveness of the protected area in terms of mitigating major threats to the species, in order to give a better indication of protected area functioning.

The poor protection afforded to native freshwater fishes by protected areas, is not unique to the CFE, but is consistent with findings from other regions including the United States (e.g., Lawrence et al., 2011; Jenkins et al., 2015; Grantham et al., 2017), Europe (e.g., Keith, 2000; Hermoso et al., 2015; Miranda and Pino-del-Carpio, 2016), South America (Azevedo-Santos et al., 2019), and Australia (Januchowski-Hartley et al., 2011). The limited protection afforded by these areas are a result of either limited representation of species, inadequate management focused towards freshwater ecosystems or a combination of both. In order to meet a set conservation targets, a species should not only be present and viable in the protected area, but the protected area must function to protect the species against significant threats. In the case of freshwater fishes of the CFE, the primary threats are non-native piscivores and loss of critical habitats or deterioration in habitat quality (Tweddle et al., 2009; Ellender and Weyl, 2014). Protected areas by their very nature are designed to safeguard against land-use impacts and land transformation, and are thus automatically protected from direct threats to habitat

TABLE 1 | Summary of protection level assessment results, with population target, number of protected areas taxa occur in, percentage target that is met, final protection level and protection level based on representation only.

Taxon	Population target	No of protected areas recorded	% of Target conserved	Protection level (representation and effectiveness)	Representation only
Pseudobarbus burchelli s.s.	5,000	2	4	Not protected	Poorly protected*
Pseudobarbus verloreni	10,000	0	0	Not protected	Not protected
Pseudobarbus skeltoni	10,000	1	15,1	Poorly protected	Poorly protected
Pseudobarbus heuningnes	10,000	0	0	Not protected	Not protected
Galaxias sp. nov. "Breede"	10,000	2	0,2	Not protected	Poorly protected*
Pseudobarbus burgi	10,000	5	25	Poorly protected	Moderately protected*
Austroglanis barnardi	5,000	3	50	Moderately protected	Moderately protected
Austroglanis gilli	10,000	13	102	Well protected	Well protected
Cheilobarbus capensis	10,000	1	0,1	Not protected	Poorly protected*
Labeo seeberi	10,000	2	10	Poorly protected	Poorly protected
Sedercypris erubescens	5,000	5	70,2	Moderately protected	Well protected*
Pseudobarbus phlegethon	10,000	5	50	Moderately protected	Moderately protected
Pseudobarbus sp. nov. "Doring"	5,000	2	40	Poorly protected	Poorly protected
Pseudobarbus asper	10,000	10	56	Moderately protected	Well protected*
Sedercypris calidus	10,000	12	110,1	Well protected	Well protected
Cheilobarbus serra	10,000	7	45	Poorly protected	Moderately protected*
Galaxias sp. nov. "Klein"	10,000	2	10	Poorly protected	Poorly protected
Galaxias sp. nov. "Riviersonderend"	10,000	5	30	Poorly protected	Moderately protected*
Galaxias sp. nov. "Goukou"	5,000	1	20	Poorly protected	Poorly protected
Galaxias sp. nov. "Heuningnes"	10,000	0	0	Not protected	Not protected
Galaxias sp. nov. "slender"	10,000	0	0	Not protected	Not protected
Galaxias sp. nov. "Verlorenvlei"	10,000	0	0	Not protected	Not protected
Labeobarbus seeberi	10,000	12	75,1	Moderately protected	Well protected*
Galaxias sp. nov. *gourits*	10,000	0	0	Not protected	Not protected
Pseudobarbus sp. nov. "Breede"	10,000	21	147,1	Well protected	Well protected
Pseudobarbus tenuis	10,000	22	190	Well protected	Well protected
Pseudobarbus sp. nov. "Forest"	10,000	13	111	Well protected	Well protected
Pseudobarbus afer	10,000	6	26	Poorly protected	Moderately protected*
Pseudobarbus tenuis "Keurbooms"	10,000	3	15	Poorly protected	Moderately protected*
Pseudobarbus senticeps	5,000	1	10	Poorly protected	Poorly protected
Pseudobarbus swartzi	10,000	5	36	Poorly protected	Moderately protected*

*An * indicates species that had a change in status due to the inclusion of effectiveness in the assessment.*

diversity and quality (Keith, 2000). This is however only true when the headwaters of the system as well as the catchment area of the river is protected. Effective conservation of riverine ecosystems thus require protection of entire catchments, which is often not feasible due to scale and existing land-use practices (Skelton et al., 1995). Historical and ongoing land transformation have resulted in major impacts on both terrestrial and aquatic habitats in lowland areas (Rouget et al., 2003a,b). Consequently, the middle and lower reaches of most rivers are impacted by unsustainable water abstraction, modification of natural flow regimes, sedimentation and pollution (Russell, 2011; de Moor and Day, 2013; Shelton et al., 2018). These impacts, coupled with widespread and established populations of non-native piscivores in mainstem habitats have resulted in highly fragmented native fish populations that persist in headwater streams that act as sanctuary areas (Chakona and Swartz, 2012).

Given the degraded state of the majority of mainstem rivers in the region, coupled with reserve bias to high altitude areas, it is expected that species rated as being "well protected" are likely to be headwater specialists or widespread species that occur in headwater habitats as well as in downstream sections of larger tributaries. This is supported by our findings as species that were evaluated as being "well protected" are mainly small-bodied minnows. Some of these are headwater specialists, such

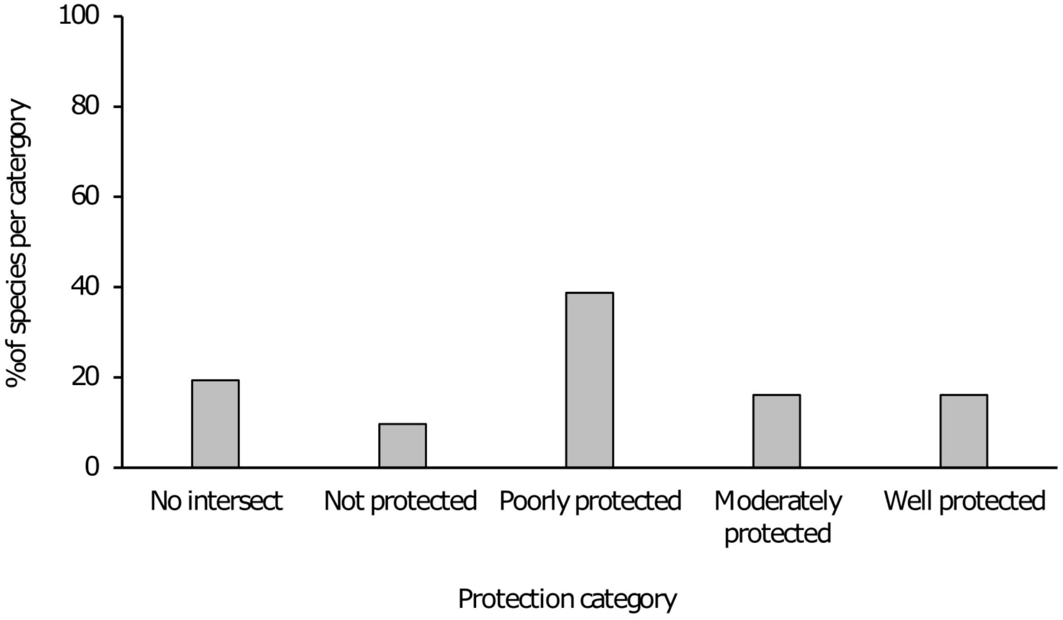

FIGURE 1 | Bar chart indicating various protection level categories and the percentage of taxa in each category.

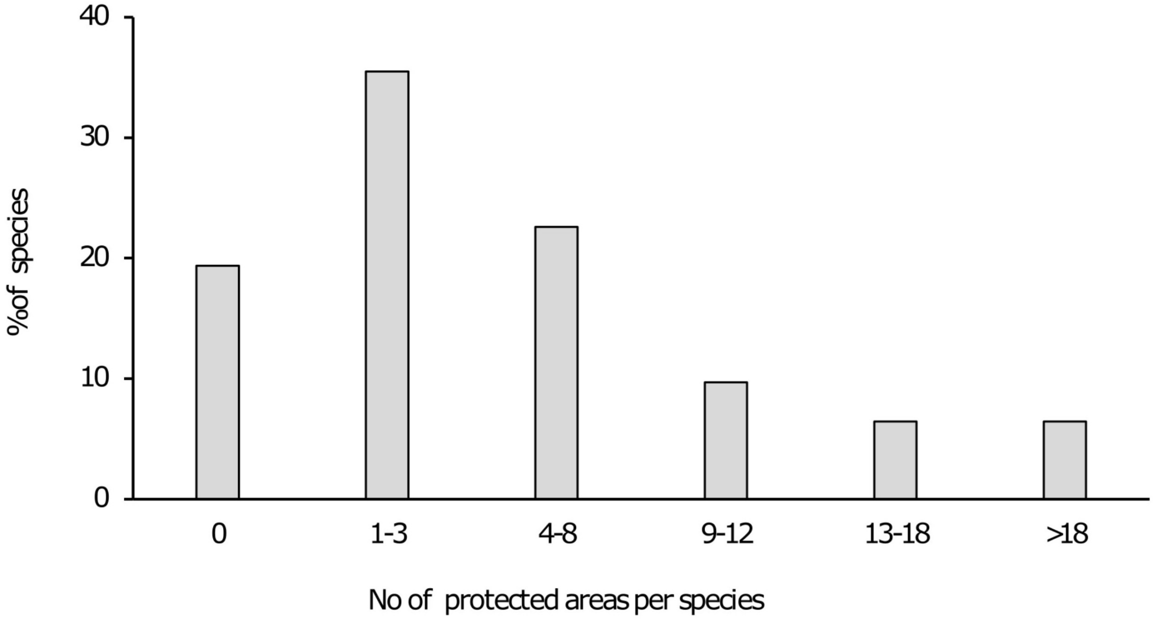

FIGURE 2 | Bar chart indicating the percentage of species present within various numbers of protected areas.

as the slender redfin *Pseudobarbus tenuis*. Others are habitat generalists which can occur in high altitude mountain streams while also extending into lower reaches of larger tributaries such as the Breede River redfin *Pseudobarbus* sp. nov. "Breede" and the Clanwilliam redfin *Sedercypris calidus*. Endemic to the Gouritz system, *P. tenuis* is present in headwater streams on at least 22 formally protected areas and the majority of these populations are viable and can be considered "well protected" based on recent surveys of Swartberg Nature Reserve Complex and associated provincial reserves. well protected headwater streams and rivers will however only serve to protect native fish fauna in the absence of predatory non-native species such as *O. mykiss* and *Micropterus* spp. The typical cool and clear headwater streams of the Cape Fold Mountains provide ideal habitat for the invasion and establishment of *O. mykiss.* This can significantly reduce the protection value of a protected area even in the absence of other

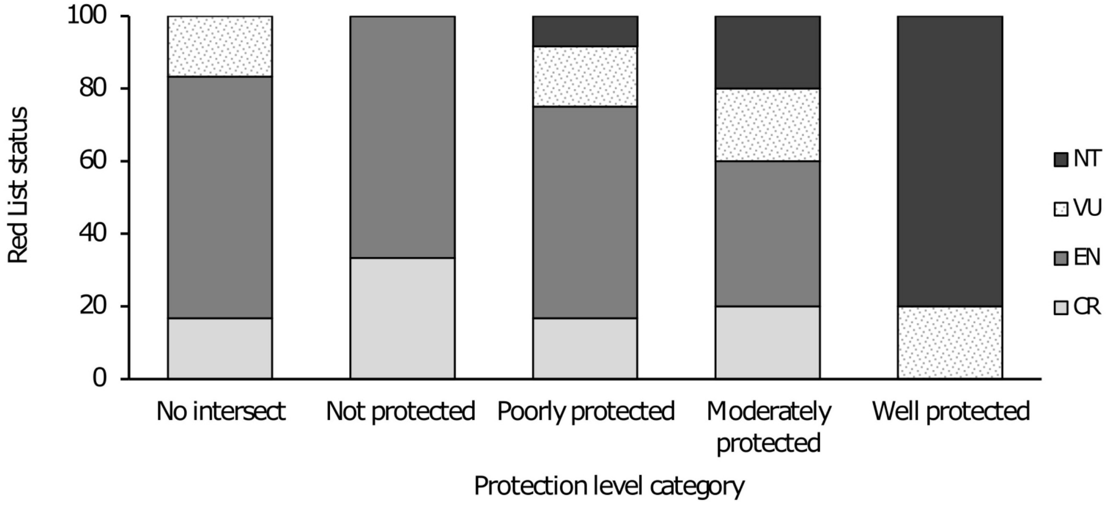

FIGURE 3 | Percentage of species within each Protection Level given each threat category.

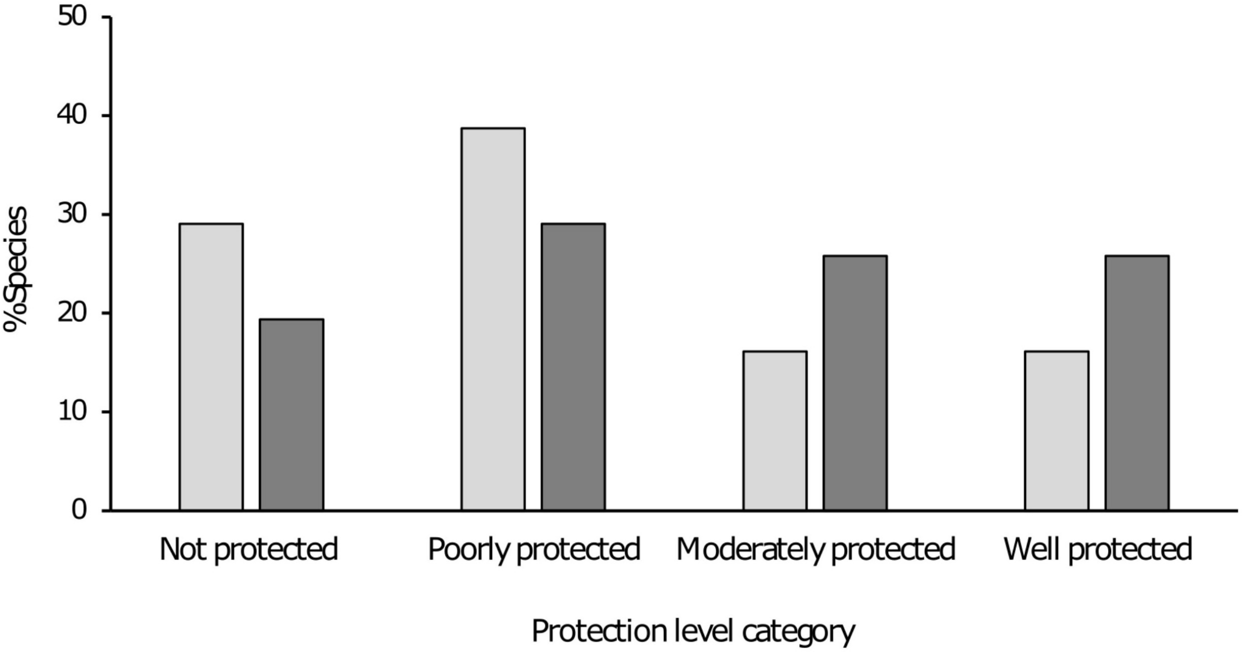

FIGURE 4 | Bar chart indicating the percentage taxa within each protection level category depending on method of assessment, protection level including effectiveness (grey), and protection level excluding effectiveness (dark grey).

threats. *Oncorhynchus mykiss* is a global invader with deleterious impacts on native biota in many parts of its introduced range (Lintermans, 2000; Morgan et al., 2004; Arismendi et al., 2009). For example, Shelton et al. (2014b) reported that in the Breede River system, *O. mykiss* significantly reduced the densities of three native fish species and completely displaced native fishes at more than 50% of the study sites. While some *Pseudobarbus* sp. nov. "Breede" populations are impacted by the presence of *O. mykiss* and other invasive fishes, many populations occur in protected areas upstream of invasion barriers, or in tributaries where *O. mykiss* have not yet been introduced, such as the Langeberg and Riviersonderend provincial reserves and their associated mountain catchment areas.

In cases of species with more restricted current distribution ranges, the presence of *O. mykiss* on protected areas may have a more significant effect. In the case of the Berg River redfin *Pseudobarbus burgi*, five of the eight known subpopulations occur on formally protected areas where the headwaters are within the protected area, thereby safeguarding against upstream impacts (Jordaan et al., 2017). However, because *O. mykiss* has become established in these protected areas, the degree of protection for *P. burgi* was evaluated as fair, resulting in the species being listed as "poorly protected." If the reserves where *P. burgi* and *O. mykiss* co-occur (Jonkershoek and Haweqwa provincial reserves and their associated mountain catchment areas) can change management objectives to remove the trout from these rivers, the protection value of these areas would increase and the species would be "moderately protected." The feasibility of *O. mykiss* removal from these rivers however remains to be determined.

Two other species that were evaluated as being "well protected," *S. calidus* and the Clanwilliam rock catfish *Austroglanis gilli*, are both endemic to the Olifants-Doring River system in the CFE. These two species have several well protected populations within the greater Cederberg Nature Reserve complex where they persist in headwater streams upstream of invasion barriers (Van der Walt et al., 2017a,b). *Micropterus* species are established invaders in the Olifants-Doring River system where especially smallmouth bass *M. dolomieu* have severely impacted native freshwater fishes in the system. Van der Walt et al. (2016) conducted a comprehensive study of *Micropterus* invasion in 41 tributaries of the Olifants-Doring River system and demonstrated the critical role that instream barriers play in restricting the movement of non-native species and thus preventing localised extinctions of native fishes in headwater streams situated in protected areas. Shelton et al. (2014a) also highlighted the important role of instream barriers in preventing upstream movement of *M. dolomieu* in the Witte River, a tributary of the Breede river system located in the Haweqwa Nature Reserve. Rahel (2013) proposed intentional fragmentation as an active management strategy in cases where non-native species pose a threat to remnant populations of native species. Typically, a barrier is constructed, followed by removal of non-native species, and reintroduction of native species into upstream segments in a strategy known as isolation management (Novinger and Rahel, 2003). This strategy was successfully implemented in the Rondegat River in the CFE where *M. dolomieu* was removed to allow a range expansion of the native fish fauna (Weyl et al., 2014). This strategy should however be evaluated within the context of potential long-term genetic impacts associated with fragmentation and isolation (Fausch et al., 2009; Chakona et al., 2020).

When considering the protection of larger cyprinids that are more reliant on mainstream habitat, the present study showed that only one species, the Clanwilliam yellowfish *Labeobarbus seeberi* can be considered to be "moderately protected." This species is endemic to the Olifants-Doring River system and occurs in 12 protected areas where it has several viable populations upstream of invasion barriers. Removal of *M. dolomieu* from the Rondegat River allowed this species to expand its range by about 4 km (Weyl et al., 2014). The two other large cyprinids endemic to this system, the Clanwilliam sandfish *Labeo seeberi* and the Clanwilliam sawfin *Cheilobarbus serra* were evaluated as being "poorly protected." However, *C. serra* is very close to meeting the criteria for "moderately protected." Although this species is present on seven protected areas, the effectiveness for some of these areas was rated as fair, given that the headwaters are not protected and thus open to potential invasion by non-native species and impacts related to poor land-use. Examples are the Winterhoek mountain catchment area where the headwaters of the Olifants River originate and the Oorlogskloof Provincial Nature Reserve with the Oorlogskloof River, which has its source closer to the town of Calvinia in the Northern Cape Province.

In contrast to *C. serra*, *Labeo seeberi* is only present in two protected areas and narrowly meets the criteria for being "poorly protected." This species was historically widespread in the Olifants-Doring system prior to the introduction of non-native fish and the construction of large instream dams such as Clanwilliam Dam (Van Rensburg, 1966; De Moor and Bruton, 1988). It now persists as a few fragmented and non-viable isolated subpopulations with the exception of the viable population in the Oorlogskloof Provincial Nature Reserve. The whitefish *Cheilobarbus capensis* (formerly *Barbus andrewi*), is currently restricted to the Breede River system and is also poorly represented within the current protected area network as it only intersects with a single protected area, Bontebok National Park. Here the mainstem Breede River is dominated by non-native fishes, and the presence and survival of *C. capensis* is uncertain. This species is listed as EN and it persists mainly within man-made impoundments outside of the formal protected area network (Impson et al., 2017).

In addition to non-native fishes, impacts associated with poor land-use practices and inadequate management of surface water resources can affect native fish populations both within and outside formally protected areas. Most of the CFE has a typical Mediterranean climate characterised by winter rainfall and hot and mostly dry summers. These climatic conditions, coupled with the water demand of a rapidly increasing population, result in severe utilisation pressure on water resources (Allsopp et al., 2014). This is not unique to the Western Cape Province, but is characteristic of many arid and semi-arid areas of the world (Collares-Pereira and Cowx, 2004). Unsustainable water abstraction can have deleterious consequences for freshwater fishes and their aquatic ecosystems, including reduced habitat, suboptimal flow and temperature conditions, restriction of migration and destruction of spawning areas (Maceda-Veiga, 2013). Species such as the smallscale redfin *Pseudobarbus asper*, which is adapted to mainstem river conditions, are especially vulnerable to excessive water abstraction, unsustainable land-use activities and anthropogenic pollution (Skelton, 2001). This species has a natural distribution range that includes both the Gouritz and Gamtoos systems and it currently occurs on 10 protected areas. Despite this, *P. asper* narrowly meets the criteria for "moderately protected" as many of the lowland protected areas where it occurs are at risk of non-native fish invasion from both upstream and downstream sources, with excessive water abstraction in upstream areas posing considerable alteration of hydrological regimes in downstream sections. Examples are the Swartberg and Anysberg Provincial Nature Reserves that both have viable *P. asper* populations, but these populations are being impacted by significant water abstraction upstream of the reserves.

Impacts related to water over-abstraction are likely to worsen in future given climate change models that predict an increasingly dry climate, with a reduced period of river flow and temperature increases, thereby reducing water quality and quantity for aquatic species such as freshwater fish (Dallas et al., 2019). Shelton et al. (2018) reported that native fish species are vulnerable to the impacts of climate change, specifically in the CFE. Climate change was however not included in the current assessment of protection level of species due to the high level of uncertainty of specific impacts on each species and how they interact within the protected areas. Future assessments need to include climate change as a threat requiring mitigation. This is possible as the National Protected Area Expansion Strategy (NPAES) includes as part of its criteria for protected area expansion the need for it to be resilient to climate change. With the recent drought (2015-present) affecting many parts of the CFE, boreholes have been installed in some protected areas in the region as precautionary measures to ensure water security in highly populated areas. However, the impact of these boreholes within protected areas are currently unknown.

Our results further illustrate that only considering species representation within protected areas and not protected area effectiveness as well, can lead to an overestimation of the value of protected areas for freshwater fishes of the CFE. This may be misleading for conservation prioritisation efforts and associated conservation interventions. The latter is highly relevant for the management of non-native fishes, which play a significant role in determining whether a protected area can function to protect fish species, as they are the main driver for reduced protection. Given the highly threatened status of the majority of freshwater fish species of the CFE, the ongoing discovery of new highly threatened lineages and the well-documented impacts of non-native fishes, there is a significant need for preventing new invasions and managing the impacts of invasions in formally protected areas. Weyl et al. (2015) highlighted the complexities associated with managing non-native fish invasions on protected areas once utilisation of a species is established. An example of conflicting management objectives is the management of introduced trout populations on Limietberg Nature Reserve for sustainability by a local angling group, which is incompatible with conservation objectives for the newly described Giant redfin *P. skeltoni*. Historically, this species was widely distributed across the Breede River system (Kadye et al., 2016), but currently it persists as three fragmented subpopulations as a result of the impacts of invasive fish. It was assessed as being "poorly protected" as well as Endangered, highlighting the need for active conservation intervention. It should also be noted, that the understanding of how multiple threats interact can assist in adaptive management decisions, and recent work using Bayesian Networks and Adverse Outcome Pathways research could be explored to improve understanding of multiple interacting threats (Mitchell et al., 2018) and provide important insights on effective management strategies.

In conclusion, the methodology used in this study can provide an indication of how well species are protected for persistence into the future, as the current protection level of a species relative to a minimum viable population is considered. Species identified as being "not protected" or "poorly protected" should, along with threatened species, be prioritised for identification and implementation of active conservation interventions and inclusion in protected area expansion processes. Acreman et al. (2019) proposed a number of actions to enhanced protected area effectiveness, most of which are applicable to the current scenario. Active conservation interventions that can be implemented on-reserve include the localised management of non-native fish to benefit highly threatened native fish fauna, coupled with the construction of barriers to prevent re-invasion (Weyl et al., 2014). These intervention measures should aim to include an active environmental awareness component to involve stakeholders, especially in the cases where so-called "conflict species" are involved. Other on-reserve management actions that will benefit freshwater fishes include the management of invasive alien vegetation to maintain intact riparian zones and to minimise the impact of fires. Forest fires are often overlooked as a threat to aquatic ecosystems but can cause significant impacts such as excessive sedimentation, bank destabilisation, changes in shading patterns and the release of toxic polycyclic aromatic hydrocarbons (Maceda-Veiga, 2013). Threats related to the alteration of flow regimes and surface water availability originate mostly outside protected areas and are therefore much more challenging to mitigate. In these cases, conservation managers are largely reliant on efficient implementation of national legislation, such as the National Water Act (Act 36 of 1998). Water use on protected areas, such as the utilisation of boreholes or diversion weirs, are mostly included in formal protected area management plans with clear goals and strategies towards sustainability and conservation of aquatic ecosystems, both on the protected area and downstream (Nel et al., 2009).

A limitation of the methodology is that some species would never be classified as "well protected" due to their small total population size and highly restricted natural distribution ranges. These species are thus not necessarily "under protected" due to the network not including them, there are merely not enough populations to meet the conservation target of 10 viable populations. Furthermore, the analysis was conducted with the best available distribution data for the species considered and for some species there are few recent records. More field surveys are required to confirm the status of populations within various protected areas and to identify pressures that may not be alleviated by the protected areas. Based on this assessment as well as the species Red List assessments, the primary threat to these species are non-native fishes. Hence improved distribution data for non-native fishes in protected areas, along with the geographical location of invasion barriers, will enhance biodiversity conservation and management in the CFE. Impacts unrelated to non-native fish such as pollution, changes in flow regimes and impacts on habitat quality may be more challenging to assess spatially, especially those located in lowland areas. Multiple stressors can also interact to produce antagonistic, additive or synergistic effects (Jackson et al., 2016). Modelling the risk of invasive species relative to other stressors should be explored to inform future assessments of protected area effectiveness. In order to test the robustness of the methodology and replicability of the results, it should be applied to other ecoregions of Southern Africa. It can also be expanded to other Mediterranean-type ecosystems such as the Iberian Peninsula that has a high number of threatened freshwater fishes and is faced with similar threats to the CFE (Maceda-Veiga, 2013). The outcome of this work should not only inform conservation planning and protected area expansion but should also form part of the development of protected area management plans and their associated monitoring and management goals. Protection level assessments of species should also be considered during Red List Assessments, as this would inform the conservation actions needed for the specific species being assessed.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

DvdC collated all datasets, contributed to the conceptualisation and write-up of the manuscript and provided comprehensive GIS support. AC contributed to the write-up of the manuscript and provided unpublished distribution data to improve the accuracy of the assessments therein. MJ contributed to the conceptualisation and collation of datasets and lead the write-up of the manuscript. All authors contributed meaningfully to this manuscript.

ACKNOWLEDGMENTS

Ms. Lize von Staden of the South African National Biodiversity Institute (SANBI) initially developed the principles of the assessment methodology used in this manuscript. Ms. Tilla Raimondo (SANBI) and Mr. Riaan van der Walt (formerly CapeNature) provided assistance and scientific inputs during the assessment process. We wish to thank the reviewers for their useful contributions which has greatly improved the quality of this work. MJ wish to thank Ms. Vicky Hudson of CapeNature for useful inputs and discussions during the write-up of this work. The authors wish to acknowledge financial support from SANBI for publication fees.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.502042/full#supplementary-material

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