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TOWARDS SUSTAINABLE MANAGEMENT OF INLAND WATERS IN TANZANIA: ASSESSING THE ECOLOGICAL INTEGRITY OF RIVER ECOSYSTEMS IN THE UPPER PANGANI RIVER BASIN (TANZANIA)

December 2020

KU LEUVEN

ARENBERG DOCTORAL SCHOOL
FACULTY OF SCIENCE

Towards sustainable management of inland waters in Tanzania: Assessing the ecological integrity of river ecosystems in the Upper Pangani River Basin (Tanzania)

Grite Nelson Mwaijengo

Supervisor:
Prof. dr. Luc Brendonck

Co-Supervisors:
Prof. dr. Bram Vanschoenwinkel
Prof. dr. Karoli N. Njau

Dissertation presented in partial
fulfilment of the requirements for the
degree of Doctor of Science (PhD):
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To God be all the Glory and Honor.

Table of Contents

List of Abbreviations

AIC:	Akaike Information Criterion
COD:	Chemical oxygen demand
CPOM:	Coarse particulate organic matter
DEM:	Digital Elevation Model
DENs:	Dendritic ecological networks
EPT:	Ephemeroptera, Plecoptera, and Trichoptera
FFG:	Functional feeding groups
FPC:	Flood Pulse Concept
FPOM:	Fine particulate organic matter
GIS:	Geographical information systems
GPS:	Global Positioning System
GSM:	gravel/sand/mud
HC:	Hydrological connectivity
HDPE:	High density polyethylene
IPCC:	Intergovernmental Panel on Climate Change
ML:	Maximum likelihood
PBWB:	Pangani Basin Water Board
PBWO:	Pangani Basin Water Office
PCA:	Principal Component Analysis
PCoA	Principal Coordinate Analysis
pRDA:	Partial Redundancy Analysis
RCC:	River Continuum Concept
RD:	Dehu River
RDA:	Redundancy Analysis
REML:	Restricted maximum likelihood
RH:	Ghona River
RMSPE:	Root-mean- square-prediction error
RRC:	Ruvu River Catchment
RS:	Soko River
RV:	Ruvu River
SASS:	South African Scoring System
SD:	Standard Deviation
SE:	Standard Error
SSNm:	Spatial Stream Network models
TARISS:	Tanzania River Scoring System
Taxa_S:	Number of Taxa
UKRC:	Usa-Kikuletwa River Catchment
UPRB:	Upper Pangani River Basin

General Introduction

“*Freshwater is a finite and vulnerable resource, essential to sustain life, development and the environment*” The Dublin Principles 1992

Rivers and streams are important freshwater ecosystems that provide a plethora of services for humans including a source of water for domestic, agricultural and industrial purposes, a source of food, a means of waste disposal, power production, transportation, and sites for the pursuit of leisure activities (Malmqvist and Rundle, 2002; Strayer and Dudgeon, 2010). Everywhere on Earth, from the smallest village to the largest metropolis the life of people is often intertwined with river ecosystems (Allan and Flecker, 1993). Although they occupy less than 1% of the earth’s land surface (Allen and Pavelsky, 2018), river ecosystems support a disproportionately large fraction of biological diversity (Allan and Flecker, 1993; Malmqvist and Rundle, 2002; Strayer and Dudgeon, 2010; Sinha et al., 2019). They also represent extensive ecotones where energy flux, complex physical structure, and flow dynamics have combined to shape the life history traits of many species (Sinha et al., 2019). Yet, rivers and streams are among the most threatened ecosystems on earth (Malmqvist and Rundle, 2002; Dudgeon et al., 2006; Strayer and Dudgeon, 2010;Vörösmarty et al., 2010). Major threats to river systems include habitat degradation, water pollution, flow modification, overexploitation, and invasion by exotic species (Allan and Flecker, 1993; Malmqvist and Rundle, 2002; Dudgeon et al., 2006). In addition, climate change is expected to have far-reaching impacts on river ecosystems (Perkins et al., 2010; Ledger and Milner, 2015). As human demand for freshwater increases globally, anthropogenic impacts on river ecosystems, and their concurrent losses of biodiversity, are increasing, with a growing concern that not only is species biodiversity being lost, but also the ecosystem services they provide (Allan and Flecker, 1993; Malmqvist and Rundle, 2002; Strayer and Dudgeon, 2010; Vörösmarty et al., 2010).

1. Tropical stream ecology

The tropical zone covers by far the largest land area of the world’s climatic regions. It encompasses a region lying between the Tropic of Cancer (23°26′12.0″ N) and the Tropic of Capricorn (23°26′12.0″ S) (Boulton et al., 2008; Lewis, 2008; Boyero et al., 2009). Tropical regions are characterized by relatively minimal seasonal temperature fluctuations (thermal stability; seasonal fluctuations increase towards the margins of the tropics), but most of them experience some degree of seasonality in rainfall which in turn governs stream hydrology (Wantzen et al., 2006; Lewis, 2008; Syvitski et al., 2014). Seasonal changes in flow regimes and hydrological connectivity noticeably regulate how tropical river systems function (Davies et al., 2008; Syvitski et al., 2014). The flood-pulse concept (FPC) (See Box 1, 2 and 3 for concepts of riverine ecosystem dynamics/stream ecosystem theory) identifies seasonal hydrology as the primary driver of ecological processes in large tropical rivers (Junk et al., 1989a). This seasonal hydrological cycle strongly influences habitat availability, aquatic food webs, and the fluxes of essential carbon and nutrients (Dallas, 2004; Douglas et al., 2005; Lewis, 2008).

Tropical flowing waters commonly have a lower oxygen reserve and a higher potential oxygen demand for a given amount of organic loading than temperate flowing water. This is because of higher water temperatures and higher metabolic rates of organisms (Lewis, 2008). Consequently, tropical flowing waters are more vulnerable to organic loading (Lewis, 2008). Tropical streams also tend to have high silica and iron contents, low ionic concentrations, less calcium and bicarbonate than sodium and chloride, and an average pH range of 4.0 to 7.5. The relatively low pH range in tropical flowing waters is a result of the low buffering capacity (low calcium and bicarbonate concentration) compared to temperate lotic systems (Payne, 1986). Dissolved forms of phosphorus and nitrogen in tropical rivers are present in quantities sufficient to support moderate to high biomass of autotrophs even under pristine conditions (Douglas et al., 2005; Davies et al., 2008; Lewis, 2008). The supplies of suspended and dissolved solids, as well as nutrients, however, span the same ranges and show the same responses to hydrology as would be expected in temperate zones (Lewis, 2008).

Box 1: The River Continuum Concept

The River Continuum Concept (RCC) conceptualizes the entire fluvial system as a continuously integrating series of physical gradients and associated biotic adjustments: “from headwaters to mouth, the physical variables within a river system present a continuous gradient of physical conditions” (Vannote et al., 1980). This gradient produces a series of responses within the constituent populations resulting in a continuum of biotic adjustments and consistent patterns of loading, transport, utilization, and storage of organic matter along the length of a river (Vannote et al., 1980). As such, rivers are seen as longitudinally linked systems in which ecosystem-level processes in downstream areas are linked to those in upstream areas. The concept further appeals that the morphological and behavioral adaptations of running water fauna reflect shifts in types and locations of food resources with stream size. Headwater streams (stream order 1st-3rd) are heterotrophic (autochthonous primary production in the headwaters is low: production/respiration (P/R) <1), dependent on allochthonous input of detritus, and the dominant consumers are shredders and collectors (see Table 1 for the different functional feeding groups amongst the macroinvertebrate communities). As stream size increases (stream order 4th-6th), the reduced importance of terrestrial organic input coincides with enhanced significance of autochthonous primary production from algae and rooted vascular plants (because of low water depth and high irradiation), and organic transport from upstream. In this portion of the continuum, the major consumer groups are collectors and grazers, and the ratio of gross primary productivity to community respiration (P/R) is >1. In large rivers (stream order > 6th), the system shifts back to a heterotrophic system as the amount of fine particulate organic matter increases (from upstream processing of dead leaves and woody debris), and the bottom consumers are predicted to be mostly collectors. The effect of riparian vegetation is insignificant, but primary production is often limited by high water depth and increased turbidity and turbulence. Such light attenuated systems would be characterized by P/R < 1. The proportion of predators remains relatively constant throughout the continuum (Vannote et al., 1980). The RCC further predicts that biodiversity of aquatic organisms is lower in the headwater regions and in the lower parts of the rivers, and that highest diversity is found in the middle reaches of the streams, where the variability of temperature, riparian influence and flow are highest and allow numerous different taxa to find their thermal optima. The concept has been, therefore, proposed as a framework for integrating predictable and observable biological features of lotic systems (Vannote et al., 1980). Fig.1 depicts the expected changes in the functional groups of invertebrates and organic matter inputs along the river continuum as indicated by the RCC.

Even though the concept was developed for natural, unperturbed ecosystems, it is believed to accommodate many unnatural, perturbed systems too. However, since its publication river ecologists have strongly argued over time on its generalization and applicability to other systems located outside the temporal and boreal regions of North America. This is possibly because physical factors such as geology, altitude, climatic-conditions, channel width and human imposed changes, which influence the structural and functional characteristics of stream communities, can vary differently in longitudinal river axes across basins and regions (Minshall et al., 1985; Sedell et al. 1989; Tomanova et al., 2007; Doretto et al., 2020). As a result, great effort has been made to set the domain of applicability of the RCC for comparing an array of streams worldwide based on their size (Minshall et al. 1992; Cushing et al. 2006), hydrology (Greathouse and Pringle 2006; Xenopoulos et al. 2017), and climate conditions (Bott et al. 1985; Minshall 1988; Jiang et al. 2011).

Box 1: The River Continuum Concept

Some of the criticism of the RCC is that it focuses almost entirely on the dynamics occurring in the mainstem of streams, without framing them within the stream network and underestimating the types and sources of discontinuities that can occur along the longitudinal gradient of a stream (Humborg et al., 1997; Maavara et al., 2015; Doretto et al., 2020). Also, the composition of biotic communities is only determined by environmental heterogeneity, while other aspects, such as dispersal capability of organisms, are disregarded. Moreover, it does not incorporate naturally occurring climatic events such as droughts (Pacheco et al., 2017) and floods (Junk et al., 1989a; Tockner et al., 2000), and human induced disturbances such as dams (Humborg et al., 1997; Maavara et al., 2015) and urbanization (Hill et al., 2017; Larsen and Harvey, 2017) which have an impact on fine sediment accumulation and the natural flow of materials along a river continuum.

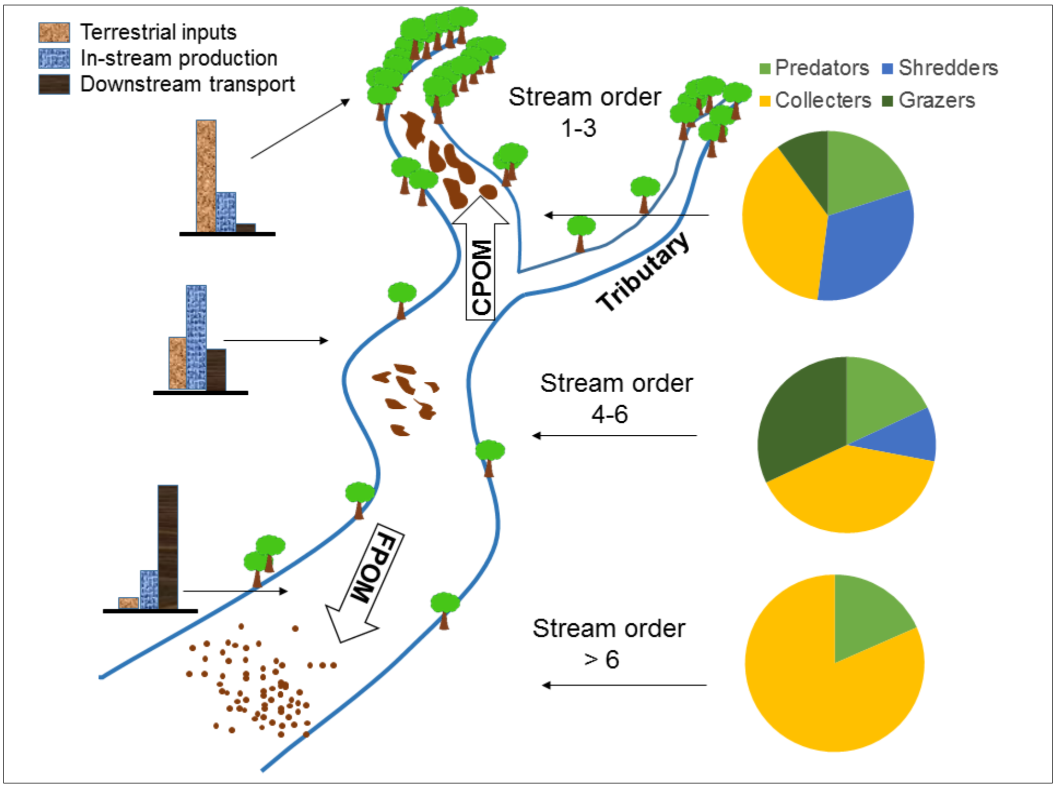


Fig.1. A hypothetical illustration of the River Continuum Concept: a proposed relationship between stream size and the progressive shift in organic matter inputs, and structural and functional attributes of lotic communities. The Pie charts on the right indicate relative abundance of benthic invertebrates in different feeding groups and bar charts on the left indicate relative importance of energy sources. CPOM and FPOM are coarse and fine particulate organic matter respectively. The figure is re-drawn after Vannote et al. (1980).

Box 2: The Flood Pulse Concept

The Flood Pulse Concept (FPC) focuses on the lateral exchange of water, nutrients and organisms between the river channel and the connected floodplain (Junk et al., 1989). The FPC promulgated the view that rivers and the fringing floodplains are integrated components of a single dynamic system, linked by strong interactions between hydrological and ecological processes. As such, the FPC introduces a lateral dimension to the dynamics of lotic systems and extends our focus beyond the main channel. The main driving force is the pulsing of river discharge that determines the degree of connectivity, productivity, and the exchange processes of organism and matter across river-floodplain gradients (Junk et al., 1989). The FPC predicts that the nutrient status of the floodplain depends on the amount and quality of suspended and dissolved solids of the parent river. Yet, it includes the premise that internal processes of the floodplain and nutrient transfer mechanisms between the terrestrial and the aquatic phase strongly influence nutrient cycles, primary and secondary production and organic matter decomposition (Junk and Wantzen, 2004). At the same time, flooding is considered as a disturbance factor that leads to a regular setback of community development and maintains the system in an immature, but highly productive stage (Junk, 1999). The river is also the refuge for aquatic organisms during low-water periods and serves as a route for active and passive dispersal. See Fig.2 for the hypothetical illustration of the FPC.

Another tenet of the FPC is that in the river- floodplain system, a large part of the primary and secondary production occurs in the floodplain habitats and that biotic diversity may be highest in the large rivers rather than in the medium sized rivers as predicted by the river continuum concept (Johnson et al., 1995; Junk and Wantzen, 2004). During a flooding, aquatic organisms migrate out of the channel and onto the floodplain to use the newly available habitats and resources. As flood waters recede, nutrients and organic matter from the floodplain are channeled back into the main channel along with newly produced biomass such as fish and invertebrates (Junk et al., 1989). As such, regular flood pulses enhance productivity in both the floodplain and the main channel and help maintain high biotic diversity in the floodplain habitats. The FPC specifies that biotic communities should exhibit a dynamic equilibrium with physical features of the flood pulse, such as duration, timing, and the rate of rise and fall in water level. Predictable flood pulses of moderate duration allow both aquatic and terrestrial organisms to adapt to the pulse. Flood pulses that are too short may not allow flood-dependent organisms to complete their reproductive cycles, while flood pulses that are too long may not allow terrestrial vegetation to develop later in the season (Junk et al., 1989).

Although the FPC was developed based upon data and long-term observations of Amazon (neotropical) and Mississippi (temperate) rivers, it provided a general structure and strengthened the premise that rivers and their floodplains have to be considered as one unit and thus cannot be treated discretely in ecological studies.

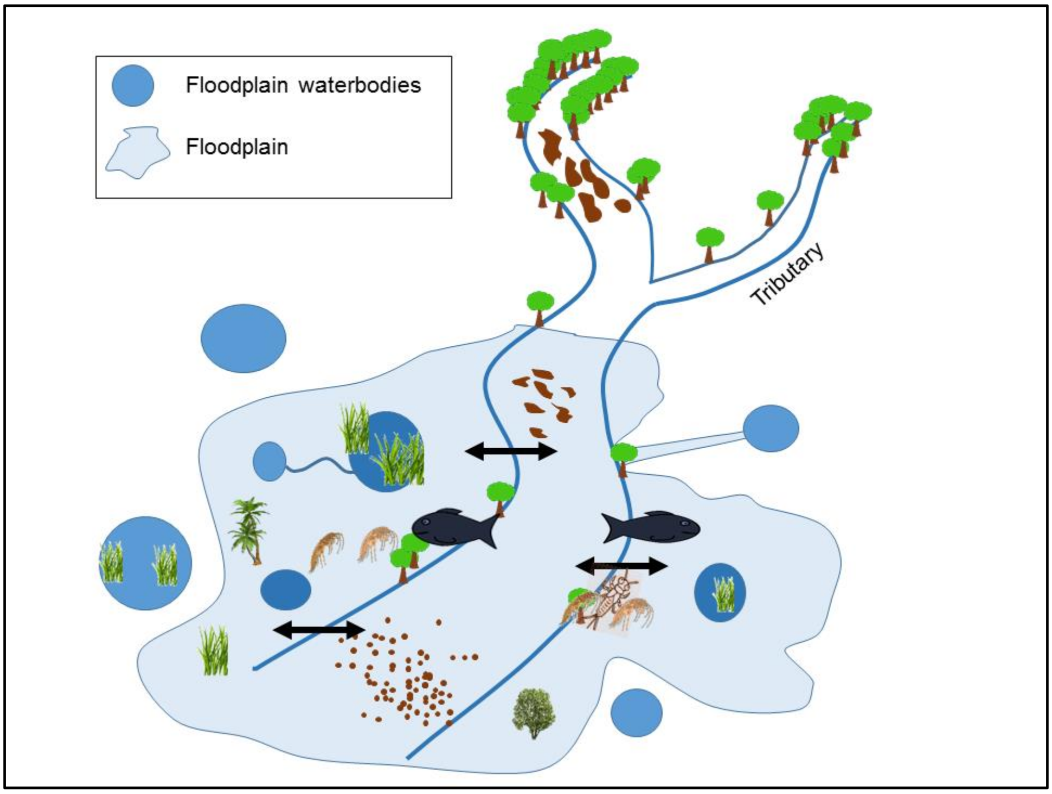


Fig.2. A hypothetical illustration of the Flood Pulse Concept (FPC) showing a lateral overflow of water from the main channel to the floodplain, and the lateral exchange of nutrients, water, and organisms between the river channel and the connected floodplain habitats.

Tropical streams have been described to contain a more diverse aquatic invertebrate fauna than their temperate counterparts (Lake et al., 1994; Boyero, 2002; Pearson and Boyero, 2009). The greater area of the tropics compared with the temperate zone and the greater climatic constancy of tropical systems and its effects, for example on resource availability, have been suggested as the major factors contributing to this resulting greater tropical diversity (Pearson and Boyero, 2009). However, studies suggest that individual taxonomic groups should be considered when examining patterns of diversity, and that more regional datasets should be used (Pearson and Boyero, 2009). The most prominent feature of tropical streams appears to be the general paucity of shredders (see Table 1 for the different functional feeding groups amongst the macroinvertebrate communities). Several authors have reported low diversity of shredders in rivers and streams in some tropical regions (e.g., Dobson et al., 2002; Douglas et al., 2005; Jacobsen, 2008; Li and Dudgeon, 2011; Dudgeon, 2012; Masese et al., 2014). Macroinvertebrate groups, such as the case-building Trichopteran Gammaridae, and Plecoptera, that dominate the detritivorous shredder guild in temperate streams are represented by very few taxa in tropical streams (Masese et al., 2014). Shredders belong to a detritivore guild in forest streams where they help in the breakdown of coarse organic matter into fine detritus making it available to filterers and collectors, and thus playing a fundamental role in organic matter decomposition and nutrient cycling

(Masese et al., 2014). The scarcity of invertebrate shredders in tropical streams has led to the conclusion that fast leaf litter breakdown is caused by high rates of microbial activity resulting from high water temperatures (Dobson et al., 2002; Pearson and Boyero, 2009; Wantzen et al., 2008; Dudgeon, 2012). As such, leaf litter decomposition and other ecosystem processes mediated by shredders in temperate streams may occur at faster rates in many tropical streams than in temperate streams, even without shredders (Wantzen et al., 2008, 2006). In addition, autochthonous energy sources may be particularly important to consumers in tropical streams, and there is some evidence of a lesser reliance on the allochthonous organic matter than in temperate streams (Wantzen et al., 2008).

Yet, even with these emerging shared characteristics, it is arguable that within the tropics there is great variability in the structure and functioning of riverine ecosystems (Wantzen et al., 2006; Boulton et al., 2008; Boyero et al., 2009), illustrating the need for broader, more representative studies, from different regions (Boyero et al., 2009). Overall, a clear picture of how tropical stream ecosystems function is lacking, and work still needs to be done on most, if not all, aspects of tropical stream ecology (Wantzen et al., 2006; Boyero et al., 2009).

Table 1 Functional feeding groups (FFGs) categorization and food resources: describing mechanisms by which macroinvertebrates acquire their food resources (adapted from Cummins et al., 2005)

Functional groups	Particle size feeding mechanisms	Dominant food resources	Food particle size range (mm)
Shredders	Cut or chew conditioned litter or live vascular plant tissues, or gouge wood.	Coarse particulate organic matter decomposing (or living hydrophyte) vascular plants	>1.0
Collectors-filterers	Suspension feeders- filter particles from the water column	Fine particulate organic matter decomposing detrital particles; algae, bacteria, and feces	0.01-1.0
Collectors-gathers	Deposit feeders- ingest sediment or gather loose particles in depositional areas	Fine particulate organic matter decomposing detrital particles; algae, bacteria, and feces	0.05-1.0
Grazers/Scrapers	Graze rock and wood surfaces or stems of rooted aquatic plants	Periphyton-attached non-filamentous algae and associated detritus, microflora and fauna, and feces	0.01-1.0
Predators	Capture and engulf prey or tissue, ingest body fluids	Prey-living animal	> 0.5

Box 3: The river wave concept

The river wave concept (RWC) lies on the premise that the wave provides a useful model for river flow. It conceptualizes river flow as a series of waves and emphasizes that the river waves drive ecosystem processes and are responsible for the structure and organization of the physical form of the river and its floodplain. The nature of river waves is influenced by geology, geomorphology, climate, and anthropogenic regulation and, in turn, influences biodiversity, the composition of riverine biota, and productivity through reciprocal feedback with geomorphological features (Humphries et al., 2014). The location and source of autochthonous production or allochthonous inputs, and the storage, transformation, and the longitudinal or lateral transport of the material and energy derived from that production and inputs, are largely a function of the temporal or spatial position (trough, crest, ascending or descending limbs) on the river wave (Humphries et al., 2014). The strengths of the RWC lie in its ability to bring together three main river ecosystem concepts/models (i.e., river continuum concept (RCC), flood pulse concept (FPC), and riverine productivity model (RPM)) and to identify to which parts of the puzzle the concepts belong. It proposes that the three river ecosystem concepts, together, complementarily explain the source of organic matter and the nature of storage, transformation, and transport of material and energy in rivers, and entails that each concept is more appropriate at different positions on the river wave.

The RWC uses the wave as a model because river flow involves the movement of water down an altitudinal gradient. It views the wave as changing river surface elevation through time at a location which occurs as a result of changing volumes of water passing that point with corresponding changes in velocity and stream power (i.e., its capacity to do work on the physical boundaries), rather than a simple rise and fall (Humphries et al., 2014). At any point in time or space, river flow may be in a trough (baseflow), ascending, descending, or at a crest (peaking or flooding). The RWC presents three hypotheses that relate to the patterns and processes associated with troughs, ascending and descending limbs, and crests of the river wave which broadly follow the principles of the RCC, FPC, and RPM. At the trough of a river wave (equates to low flow or baseflow), the RWC hypothesizes that the local production of autochthonous and local allochthonous inputs contribute most to stream metabolism and that significant local transformation of these materials through decomposition and assimilation at various trophic levels occur, whereas the transport of materials from upstream is limited, which approximates the predictions of the RPM (Thorp and Delong, 1994). On the ascending or descending limbs of river waves (equate to rising and falling hydrographs), the RWC hypothesizes that upstream allochthonous inputs and longitudinal transport of material and energy predominate, whereas local production, inputs, storage, and transformation are of lesser importance, and that the RCC is the most appropriate of the existing models (Vannote et al., 1980). As the river wave rises to a crest (equate to flood flows in rivers), the RWC hypothesizes that the contribution of allochthonous inputs of material and energy from floodplain habitats by lateral transport and then by autochthonous floodplain production dominates in rivers. The storage and transformation of material play important roles, although upstream allochthonous production and transport continue to be substantial, and that the FPC is the most appropriate of the existing models (Junk, 1999). The RWC, thus, allows predictions to be made and hypotheses to be tested, relating to the sources, storage, transformation, and movement of material and energy in rivers at different positions on the hydrograph: for rivers whose waves differ in their shape, amplitude, wavelength, or frequency, and for rivers with natural or altered flow regimes (Humphries et al., 2014).

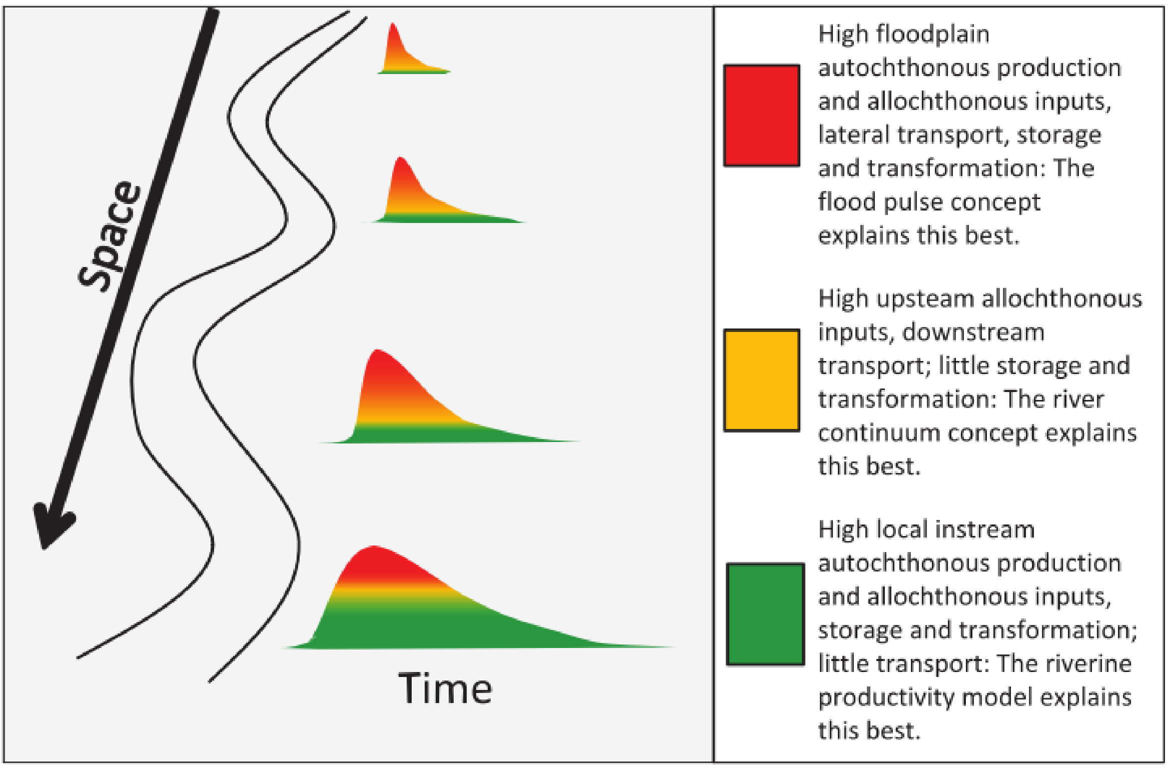


Fig.3. Hypothetical examples of the variation in time and space of river waves and the relative importance of troughs, ascending and descending limbs, and crests to allochthonous inputs, autochthonous production, transport, storage, and transformation of material and energy. From Humphries et al. (2014).

2. Spatial and temporal scale variation in river systems

Rivers are hierarchical systems having characteristics evident over a variety of spatial scales: ranging from microscale habitat (e.g., gravel, wood, or leaf detritus in a stream segment) to the macroscale habitat (i.e., entire watershed) (Frissell et al., 1986; Allan, 2004). A micro-scale habitat is contained within a river segment which is part of the catchment of a single tributary stream, and which in turn often is part of a larger watershed made up of many such tributaries and encompasses the terrestrial land area within the drainage basin (Frissell et al., 1986; Allan et al., 1997) (Fig.4). Processes occurring at multiple spatial scales often interact, creating hierarchical correlated changes in river communities and ecosystem characteristics (Frissell et al., 1986; Allan et al., 1997; Tudesque et al., 2014; Dalu et al., 2017) (Chapter 2). This is in accordance with the hierarchy theory which predicts that physical, chemical, and biological variables at a small spatial scale are constrained by other variables at larger spatial scales (Allen and Starr, 1982). Frissell et al. (1986) encapsulated this idea for stream and river systems and stated that microscale patterns are constrained by macroscale geomorphic patterns. For example, water chemistry and sediment yield are primarily governed by geology, hydrology, soils, and vegetation at the watershed scale (Allan et al., 1997; Vondracek et al., 2005; Richards et al., 1996), however, riparian vegetation (see Box 3 for some of the most important terms used in river studies) can mediate sediment and nutrient inputs to streams (Vondracek et al., 2005; Rios and Bailey, 2006). Riparian vegetation also affects the timing and amount of discharge, instream water temperature, quantity and quality of allochthonous material, and influences habitat structure, channel morphology, and hydraulic complexity (Allan et al., 1997; Allan, 2004; Vondracek et al., 2005). As such changes occurring at any spatial scale can affect the structure and quality of stream habitats, food resources, and the overall stream community structure (Sliva and Williams, 2001; Wang et al., 2003; Allan, 2004; King et al., 2005).

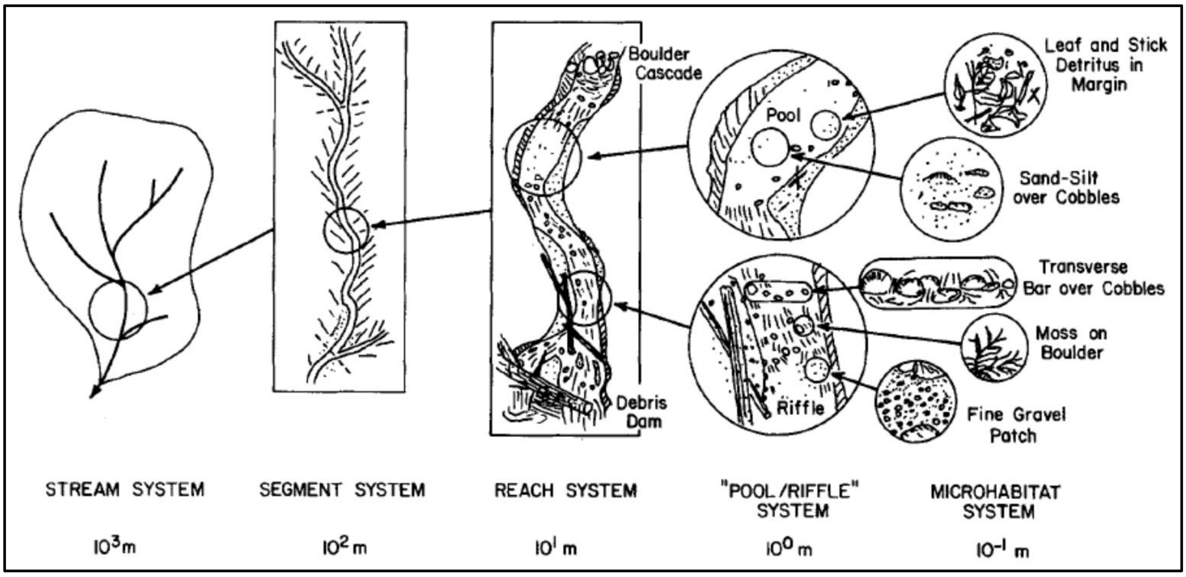


Fig.4. Hierarchical organization of river systems and habitat subsystems: from the largest spatial scale of landscape or watershed to successively smaller scales of the valley segment, stream reach, individual channel units (i.e., pools and riffles) and microhabitat units (i.e., gravel, wood or leaf detritus). From Frissell et al. (1986).

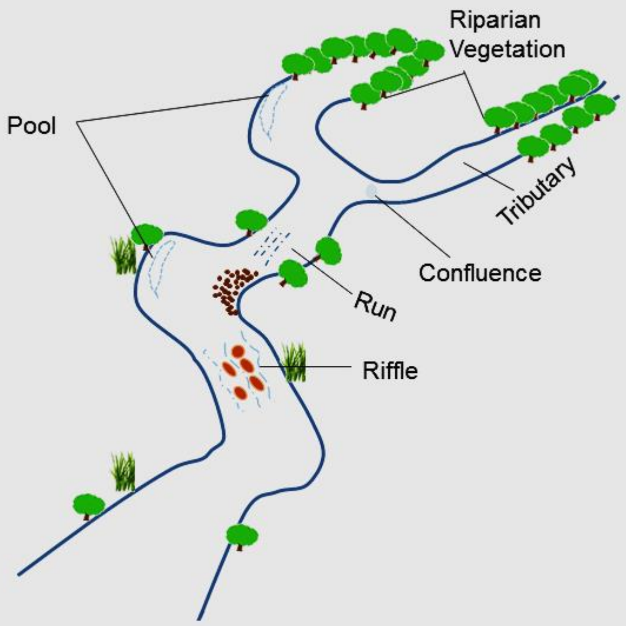
Studies investigating the relationships between river quality and the surrounding landscape at different spatial scales have produced inconsistent results. Some studies have shown that watershed landscape variables are better predictors of stream water quality and community assemblage (Roth et al., 1996; Allan et al., 1997; Sliva and Williams, 2001; King et al., 2005; Tudesque et al., 2014). In contrast, other researchers have found that landscape variables at a local scale (reach or riparian scales) are the best predictors of river quality conditions (Richards et al., 1997; Lammert and Allan, 1999; Meador and Goldstein, 2003; Stanfield and Kilgour, 2012; Shi et al., 2016). In addition, other studies have found that both local scale and watershed landscape variables predict community structure equally (Morley and Karr, 2002; Weigel et al., 2003). The majority of studies examining the relationships between river quality and landscape at multiple spatial scales, however, have been conducted in the temperate region (e.g., Allan, 2004; King et al., 2005; Schiff and Benoit, 2007; Tran et al., 2010; Wang et al., 2014). Studies are needed in regions with differing biogeographic and biophysical characteristics to develop general or comparative models on the multi-spatial scale relationships between landscape and river quality. In addition, in the scope of river monitoring and conservation, understanding at which scale the surrounding landscape and human disturbances affect river quality at a given point is essential to adapt scale-appropriate strategies to protect and rehabilitate river ecosystems (Tudesque et al., 2014).

Besides the spatial scale, river ecosystem structure, and function are also dependent on changes at the temporal scale (Dallas, 2004; Allan and Castillo, 2007) (Chapter1). Tropical flowing waters show well-defined seasonality in water depth, flow velocity, and water chemistry (Poff et al., 2006; Kizza et al., 2009; Kilonzo et al., 2014). Because temperatures remain relatively uniform at a given tropical locality, seasonal variability is based primarily on changes in precipitation patterns (rather than precipitation in conjunction with temperature) which accounts for seasonal differences in hydrology, resulting in the formation of dry and wet seasons (Lewis, 2008; Kizza et al., 2009). The variation in precipitation induces variations and changes in water quality, habitat quality, and the composition of biological communities and ecosystem functioning (Fisher et al., 2001; Kilonzo et al., 2014). For example, the high precipitation during the wet season can either decrease the chemical concentrations by dilution or increase concentrations and/or loadings of various pollutants including total suspended solids, nutrients and microorganisms by runoff (Kilonzo et al., 2014; Kalkhoff et al., 2016; Nhiwatiwa et al., 2017; Rostami et al., 2018). Heavy rainfalls, especially after a long dry period, accumulate pollutants in runoff pathways which are ultimately discharged into rivers (Rostami et al., 2018). In addition, variation in discharge often translates into differences in wetted perimeter, hydraulic conditions, and biotope availability. For example, stony bottom biotopes such as runs become riffles under low-flow conditions, and marginal vegetation may change from lotic to lentic (Dallas, 2004).

Seasonal variation in hydrological and hydraulic variables directly influences the occurrence and distribution of riverine biota between seasons. Different benthic macroinvertebrate taxa, for example, show a preference for the dry or the wet period (Kaaya, 2014). High-flow events during the wet season are one of the most predominant forms of natural disturbance in tropical river systems. They have the potential to remove benthic communities and reduce the food resources by carrying away benthic detritus and scouring benthic algae (Jacobsen et al., 2014). As such tropical riverine communities have adapted strategies to deal with temporal changes in hydrology that drive major shifts in the availability of habitats and food resources. Benthic macroinvertebrates, for example heptageniid and baetid mayflies (Ephemeroptera), have developed multivoltine life cycles (i.e., production of multiple generations per year) (Dudgeon, 1996; Yule and Pearson, 1996; Salas and Dudgeon, 2003; Dallas, 2004; Pearson and Boyero, 2009). Seasonal variation in discharge also influences macroinvertebrate drift (See Box 5) which in turn affects the abundance, composition and distribution of macroinvertebrates in river systems (Naman et al., 2016). Interestingly, mixed results have been reported when examining temporal changes in tropical macroinvertebrate community composition, with some studies reporting temporal differences (e.g., Ndaruga et al., 2004; Leung and Dudgeon, 2011; Kilonzo et al., 2014; Keke et al., 2017) while others temporal stability (e.g., Tumwesigye et al., 2000; Baptista et al., 2001; Mesa, 2010). However, in both studies' macroinvertebrate abundances were negatively affected by the increase in precipitation.

Box 4: Summary of important terms used in river studies

Keywords	Definitions
Drainage basin	The area of land that is drained by a river and its tributaries
Catchment area	The area within the drainage basin
Watershed	An area of land whose total surface drainage flows to a single point in a river
Source	The beginning or start of a river
Mouth	The point where the river comes to the end, usually when entering a lake or the sea
Tributary	A stream or smaller river which joins a larger stream or river
Confluence	The point at which two rivers or streams join
Floodplain	The wide, flat land of the river valley consisting of sediments (alluvium) deposited by the river. The floodplain is usually found in the lower course of a river and periodically flooded when the river flow exceeds the channels' carrying capacity.
Pool	A reach of a stream that is characterized by deep, low-velocity water and a smooth surface.
Riffle	A reach of stream that is characterized by shallow, fast-moving water broken by the presence of rocks and boulders
Run	A reach of stream characterized by fast-flowing, low turbulence water; connecting riffles and pools
Upstream	Opposite to the currents flow, towards the source of the river
Downstream	The direction that the river flows, towards the mouth of the river
Riparian - vegetation	The plants that grow adjacent to a river or stream, and rely upon the hydrology of the associated river/stream
Reach	Any defined length of river.



Box 5: Invertebrate drift

Drift is a term that defines the downstream transport of organisms such as aquatic invertebrates, terrestrial invertebrates (falling inside the river), and pieces of vegetation and debris in lotic systems (Allan and Russek, 1985; Brittain and Eikeland, 1988; Gibbins et al., 2007b; Naman et al., 2016). Aquatic invertebrates can be transported downstream in response to predation, competition, water physicochemical changes (temperature and discharge, or changes induced by anthropogenic disturbances), or passively by life histories and circadian rhythms (Brittain and Eikeland, 1988; Naman et al., 2016; Mendoza et al., 2018). For invertebrates, drifting may be a mode of patch selection balancing resource acquisition and predation risk. At the population level, drift can influence spatial population structure by linking populations through dispersal and may also represent a form of density-independent emigration or density-dependent self-thinning (Brittain and Eikeland, 1988; Naman et al., 2016). In a broader ecosystem context, drift constitutes a key trophic pathway in streams, providing the prey base for a diverse guild of fishes adopting a specialized central place drift-foraging strategy (Naman et al., 2016). Several drivers of drift have been identified and have led to various categories of drift that have been used in the literature (e.g., behavioral drift, distributional drift, constant drift) (Brittain and Eikeland, 1988). At a broad level, drift can be partitioned into (i) passive drift, where organisms accidentally lose purchase from the substrate due to hydraulic stress, and (ii) active drift, where organisms deliberately leave the substrate to enter the water column (Sagar and Glova, 1992; Gibbins et al., 2007a,b; Miller and Judson, 2014; Naman et al., 2016). Passive drift occurs via mechanical dislodgement from the substrate because of near-bed shear stress and often results from increases in discharge or turbulence, which may be associated with substrate mobilization (Brittain and Eikeland, 1988; Gibbins et al., 2007b; Naman et al., 2016). Catastrophic drift (mass drift) is defined as a rapid increase in passive drift which is usually associated with several flow-related thresholds (e.g., flood conditions during which the substrate is physically disturbed by high discharge), or other extreme factors, such as pesticides, heated waters and drought (Brittain and Eikeland, 1988). Active drift, in contrast, results from deliberate behaviors, including benthic predator avoidance, active patch selection while foraging, or escape from unfavorable abiotic conditions. Density-dependence may also increase drift entry owing to increased competition for space or resource limitation (Brittain and Eikeland, 1988; Miller and Judson, 2014; Naman et al., 2016). Invertebrate drift is not constant, but varies with season, from day to day and during the day (Cowell and Carew, 1976; Sagar and Glova, 1992; Boyero and Bosch, 2002; Barbero et al., 2013; Mendoza et al., 2018). Variation in drift during the day may give rise to diel periodicity; defined as a recurrent pattern with a period of 24 hours (Brittain and Eikeland, 1988; Sagar and Glova, 1992; Mendoza et al., 2018). Studies have shown that drift increases during the night, especially during the period just after sunset and to a lesser extent before sunrise (Elliott, 1969; Sagar and Glova, 1992; Mendoza et al., 2018). The direction and magnitude of seasonal trends varies among studies. For temperate streams, drift abundance appears to peak in spring and declines through the summer and fall (Brittain and Eikeland, 1988; Elliott, 1969; Naman et al., 2016). In contrast, tropical streams show generally less consistent seasonal patterns (Cowell and Carew, 1976; Mathooko and Mavuti, 1992; Boyero and Bosch, 2002). This difference may be a result of biotic processes unique to tropical streams (i.e., continuous benthic invertebrate reproduction associated with reduced seasonality and precipitation-induced flood events), but may also reflect the deficit of studies in the tropics relative to temperate systems (Naman et al., 2016).

3. Connectivity and spatial pattern in river and stream networks

Stream networks are inherently dendritic (dendritic ecological networks (DENs)) consisting of headwater streams connected by larger mainstem channels (Fagan, 2002; Grant et al., 2007; Brown and Swan, 2010; Peterson et al., 2013; Seymour et al., 2015). ‘Dendritic’ describes the geometric pattern of arborescent bifurcation, consisting of a ‘mainstem’ and ‘branches’ which decrease in size and increase in number hierarchically as one proceeds upwards through the network (Grant et al., 2007), see Fig.5 for schematic illustration of the dendritic river networks. The unique branching geometry of stream networks distinguishes riverine systems from other ecological networks and influences the ecological patterns and processes in these systems (Ganio et al., 2005; Grant et al., 2009; Brown and Swan, 2010; Peterson et al., 2013). The movement of organisms, material and energy is primarily constrained to the physical network, which forms ecological corridors (Ganio et al., 2005; Peterson et al., 2013; Isaak et al., 2014). For example, the availability and spatial arrangement of instream habitats influence species distribution, while the branching structure of the network affects in-stream dispersal to those habitats and resulting biotic interactions (e.g., predation and competition). In addition, the land area drained by a stream network provides nutrient inputs to streams (i.e., lateral connectivity), where instream processes alter the form and concentration of those nutrients, which are then transported downstream (i.e., longitudinal connectivity) (Peterson et al., 2013).

Given the unique characteristics of DENs and the spatial complexity of processes in the physical network, many analytical methods used to quantify relationships in other ecological systems are unsuitable for studying the influence of network structure and connectivity on physical, chemical and biological processes in these systems (Fagan, 2002; Grant et al., 2007; Peterson et al., 2013). Statistical methods commonly used to examine DEN data, either ignore the network structure, connectivity and directionality of the network, or assume that proximity and connectivity are adequately described using Euclidean distance (Peterson et al., 2013; Isaak et al., 2014). For example, most of the statistical techniques applied to data measured on river networks were developed for terrestrial applications and are not optimized for rivers and streams. However, rivers are fundamentally different from their terrestrial counterparts because they consist of directed networks that channel flows of energy and materials through narrow corridors within terrestrial landscapes (Isaak et al., 2014). In addition, as sampling locations occur closer in space, the assumption in classical statistics of independence among observations may be violated, and poor parameter estimation and statistical inference could result (Ganio et al., 2005; Isaak et al., 2014). A better choice is to use spatial statistical methods that incorporate the distance between data points into the analysis to account for correlation among nearby values (spatial autocorrelation), thus, increasing precision of the statistical inference (Ganio et al., 2005; Peterson and Ver-Hoef, 2010; Ver-Hoef and Peterson, 2010; Isaak et al., 2017) (Chapter 3).

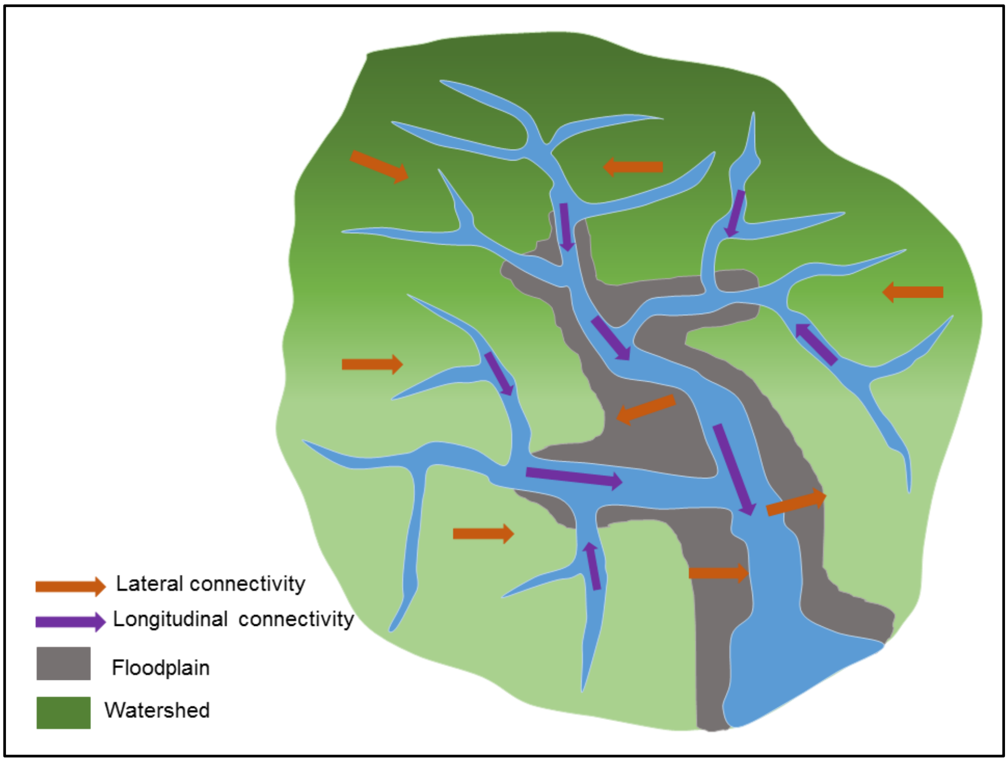


Fig.5. Schematic illustration of the dendritic river network and lateral and longitudinal connectivity.

Despite the apparent recognition that the spatial configuration of stream networks can be an important determinant of ecological patterns and processes, there has been little research directly addressing this topic. Only a few studies have explicitly considered the branching patterns of stream networks (e.g., Brown and Swan, 2010; Frieden et al., 2014; Isaak et al., 2017; Jackson et al., 2018; Kuemmerlen et al., 2019). Therefore, this specifies that a more spatially explicit examination of stream networks is needed, particularly in different watersheds and regions.

4. Temporary wetlands in the river-floodplain ecosystems

"We all interact with and depend on wetlands for our livelihoods, sustenance and well-being" Ramsar Convention on Wetlands, 2018.

Wetlands are among the most diverse and productive ecosystems on earth (Keddy, 2010; Mereta et al., 2012; Ramsar Convention Secretariat, 2016). They are cradles of biological diversity, providing the water and primary productivity upon which countless species of plants and animals depend for survival and serve as transmission pathways for species and life stages of organisms primarily adapted to other ecosystems. Although wetlands cover about 6% of the world's land surface (Mitsch and Gosselink, 2000; Wang et al., 2012; Junk et al., 2013), they contribute up to 40% of the annual global ecosystem services (Costanza et al., 1997; Mereta et al., 2012). Wetlands are 'ecotones'–transitional habitats between terrestrial and aquatic ecosystems, which have a diverse mixture of habitats derived from both ecosystems (Decamps and Naiman, 1990; Shine and De Klemm, 1999): as a result they perform a wide variety of ecological functions, including carbon sequestration, water storage, nutrient cycling, flood reduction and sediment trapping (Richardson, 1994; Costanza et al., 1997; Mitsch and Gosselink, 2000; Mereta et al., 2012; Van Den Broeck et al., 2015), and are now recognized as the kidneys of the landscape or ecological supermarkets (Mitsch and Gosselink, 2000; Chen et al., 2018). As no life can exist without water, the supporting services of wetlands are irreplaceable.

In a general term, wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, permanently or temporarily during the year, and which land in normal circumstances supports or would support vegetation typically adapted to life in saturated soil. The period in which the soil can retain water above or below the surface is the primary factor determining the occurrence of wetlands and the types of flora and fauna living in them. Article 1.1 of the Ramsar Convention 1971 defines wetlands rather broadly as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water, the depth of which at low tide does not exceed six metres" (Ramsar Convention Secretariat, 2016). Five major wetland types are generally recognized: marine (coastal wetlands including coastal lagoons, rocky shores, seagrass beds and coral reefs); estuarine (including deltas, tidal marshes and mudflats, and mangrove swamps); lacustrine (wetlands associated with lakes); riverine (wetlands along rivers and streams); palustrine (meaning "marshy" – marshes, swamps and bogs) (Ramsar Convention Secretariat, 2016). Both definitions above include a broad spectrum of aquatic environments, but this study deals with a subset of wetlands: temporary floodplain wetlands (Chapter 4).

Temporary wetlands are aquatic habitats characterized by a recurrent dry phase of varying duration (Williams et al., 2001). They are unique and diverse ecosystems variable in shape, size, and depth (i.e., from tiny puddles that may hold water for a few days after rain, to more semi-permanent waterbodies that may only dry up for a few weeks in most years) (Brendonck and Williams, 2000; Williams, 2006; Boix et al., 2016). They occur in many parts of the world but are well represented in the arid and semi-arid regions (Williams, 1996; Brendonck and Williams, 2000; Rhazi et al., 2001). In tropical river systems, the alluvial floodplain may comprise a mosaic of different temporary aquatic habitats. They include isolated endorheic wetlands and floodplain wetlands (Ward and Stanford, 1995; Amoros and Bornette, 2002; Gallardo et al., 2014; Dube et al., 2019). Endorheic (depression) wetlands are inland aquatic ecosystems with closed (or near-closed) basins which increase in depth from the perimeter to a central area of greatest depth within which water accumulates (Ollis et al., 2015), while floodplain wetlands occur mostly on flat or gently-sloping land adjacent to and formed by an alluvial river channel and are subject to periodic connection with the river channel flows (Dube, 2017).

Temporary wetlands provide a number of services to humans, including water availability, water storage for grazing and agriculture, source of pasture for livestock, and harvesting of medicinal plants (Scoones, 1991; Williams et al, 2001; Rhazi et al., 2012). They also play important roles in the landscape such as for nutrient recycling, flood control, groundwater recharge, and removal of toxicants (Williams, 2006). Due to their relatively small size and shallow depth, however, temporary wetlands are vulnerable to anthropogenic impacts, including pollution and land-use changes (Nicolet et al., 2004; Rhazi et al., 2012; Van Den Broeck et al., 2015; Nhiwatiwa and Dalu, 2016) and are often regarded as good early warning systems for biological impacts of shifting climate (Waterkeyn et al., 2008).

Temporary aquatic habitats are home to unique flora and fauna, thus contributing enormously to local and regional biodiversity (Williams et al., 2003; Nicolet et al., 2004; De Meester et al., 2005): in some cases exceeding that of other bigger and permanent aquatic habitats (Williams et al., 2003; De Meester et al., 2005; Rowan, 2010). These temporary aquatic habitats provide (transient) housing to both general opportunistic species (from adjacent terrestrial or aquatic environments) and temporary wetland-specific species that are adapted to living under extreme environmental conditions (including time stress for development, reproduction, and mechanisms to bridge dry periods) (Williams, 1996; Brendonck and Williams, 2000; De Meester et al., 2005; Van Den Broeck et al., 2015). These organisms include crustaceans (large branchiopods, ostracods, cladocerans, and copepods), macroinvertebrates (gastropods, insects, and water mites), rotifers, amphibians, and macrophytes (see Fig. 6 examples of macroinvertebrates inhabiting the river systems and temporary wetlands in the upper Pangani River Basin, Tanzania). Temporary wetlands also constitute important migration corridors and feeding and breeding grounds for many birds and wildlife (Williams, 2006). In general, temporary wetland inhabitants have developed strategies to deal with the recurring dry period (which can last from a few days to several months) either through the production of drought-resistant stages (e.g., macrophytes, zooplankton, and large branchiopods) (Brendonck, 1996; Brendonck and De Meester, 2003) or to actively disperse (e.g., insects and amphibians) to nearby more permanent water bodies to escape the dry phase (Williams, 2006; Boix et al., 2016).

Besides the alternating wet-dry phases, local abiotic (e.g., hydroperiod, water quality, soil structure and composition), and biotic (e.g., competition, predation) and regional (e.g., isolation/connectivity) factors jointly influence the development and community assemblage and diversity of flora and fauna in temporary wetlands (Williams, 2006; Waterkeyn et al., 2008; Nhiwatiwa et al., 2011; Nhiwatiwa and Dalu, 2016). Hydroperiod (length of the inundation period), for example, is commonly indicated as one of the most important local habitat factors determining invertebrate community processes in temporary wetlands (Brooks, 2000; Waterkeyn et al., 2008; Boven and Brendonck, 2009; Vanschoenwinkel et al., 2009; Bagella et al., 2010), and is often linked to pool morphometry (i.e., pool area, depth), soil type (i.e., clay, sand), and local climate (Brooks and Hayashi, 2002; Bauder, 2005; Williams, 2006; Waterkeyn et al., 2008). Wetlands with longer hydroperiod provide more time for community development, successful colonization, and offer chances for recruitment by a more diverse set of taxa (Brooks, 2000; Boven and Brendonck, 2009). In addition, physical and chemical water quality properties such as conductivity (i.e., the total concentration of ions in the water), dissolved oxygen, pH and nutrient levels are also important local environmental factors indicating the suitability of the particular inundation for hatching, growth, and reproduction of invertebrates in the temporary wetlands (Waterkeyn et al., 2008, 2009; Nhiwatiwa and Dalu, 2016).

Hydrological connectivity is considered the main regional factor driving ecological functioning and biodiversity patterns in river-floodplain ecosystems (Junk et al., 1989; Amoros and Bornette, 2002). Floodplain is a flat land area adjacent to a river channel composed of unconsolidated sedimentary deposits (alluvium) and subject to periodic inundation by the lateral overflow of the river. Lateral hydrological connectivity denotes the link between the main channel of a river and the various aquatic habitats lying in the alluvial floodplain (Amoros and Bornette, 2002; Paillex et al., 2007). Pulsing of the river (see Box 2) discharge creates hydrological gradients through the floodplain resulting in connections of the river and associated floodplain wetlands (Junk et al., 1989a; Ward and Stanford, 1995). Such lateral hydrological connectivity promotes the exchange of organisms, energy and matter between the river channel and floodplain wetlands thereby influencing the biodiversity and productivity of the entire floodplain (Tockner et al., 1999; Amoros and Bornette, 2002; Gallardo et al., 2014; Dube et al., 2019). Increased hydrological connectivity between the river and associated floodplain wetlands tends to provide wetlands with sediment and nutrient-rich water, in contrast, wetlands that are infrequently flooded tend to accumulate dissolved salts and organic materials (Junk et al., 1989; Tockner et al., 1999a; Thomaz et al., 2007; Weilhoefer and Pan, 2008). Studies have shown that different biotic assemblages respond to hydrological connectivity in quite different ways, depending on their habitat requirements (Tockner et al., 1999; Gallardo et al., 2014). But overall invertebrate species diversity in temporary floodplain wetlands tends to be relatively higher at intermediate hydrological connectivity (Ward and Tockner, 2001; Paillex et al., 2007).

River connected wetlands (floodplain wetlands) tend to be colonized by fish and other invertebrates originating from the river during flooding (Junk et al., 1989; Nhiwatiwa et al., 2011; Dube et al., 2019). The presence of fish has a major structuring effect on invertebrate communities of the floodplain wetlands, through predation on vulnerable species. For example, large branchiopod crustaceans tend to be absent in floodplain wetlands (Nhiwatiwa et al., 2011; Dube et al., 2019) whereas small crustaceans have plastic mechanisms to reduce the predation risk (Dube et al., 2019). In contrast, isolated endorheic wetlands are normally fishless, they lack connectivity to a water source with fish (e.g., river) which excludes most fish. However, this does not mean that endorheic wetlands are ‘enemy-free’ (Spencer et al., 1999; Brendonck et al., 2002; Waterkeyn et al., 2016). Predation by invertebrates and amphibians has shown to be an important biotic stress factor regulating temporary wetland communities (Spencer and Blaustein, 2001; Brendonck et al., 2002; Boix et al., 2006). Studies on temporary wetlands have revealed turbellarians, notonectids, amphibian larvae, dragonfly larvae, diving beetles and notostracans to be among the top predators (Brendonck et al., 2002; Boix et al., 2006; Waterkeyn et al., 2011a). For example, notostracans (tadpole shrimps) can effectively prey on microcrustaceans (Boix et al., 2006; Waterkeyn et al., 2011a) and dormant eggs buried in the sediment (Waterkeyn et al., 2011b).

Fig. 6. Examples of macroinvertebrates inhabiting the river systems and temporary wetlands in the Upper Pangani River Basin (UPRB), northeastern Tanzania. From left to right, then top to bottom: *Potamonautes* sp. (Decapoda), *Silvatares* sp. (Trichoptera), *Afrobrianax* sp. (Coleoptera), *Anax* sp. (Odonata), *Gyrinus* sp. (Coleoptera), *Caenis* sp. (Ephemeroptera), *Marsupiobdella* sp. (Hirudinea), *Branchipodopsis* sp. (Anostraca), *Laccotrephes* sp. (Hemiptera), *Streptocephalus* sp. (Anostraca). Photographs by Grite N Mwaijengo and Emilie Hermans.

5. Biological indicators of ecosystem health

Biological indicators are living organisms whose status reflects or predicts the condition(s) of the environment (or a part of the environment) where they are found (Li et al., 2010; Lopez-Lopez and Sedeno-Diaz, 2015; Siddig et al., 2016). They are used to assess the condition of the environment or to monitor trends in condition over time (Siddig et al., 2016). Biological indicators can provide an early-warning signal of ecological problems, and can be used to diagnose the cause of an environmental problem (Dale and Beyeler, 2001; Li et al., 2010; Siddig et al., 2016). The use of biological indicators relies on the assumption that the presence or absence of, and variations in, these indicators reflect changes taking place at various levels in the ecological hierarchy, from genes to species and finally to entire regions (Li et al., 2010; Siddig et al., 2016). Moreover, biological indicators integrate overall habitat quality over long time periods and therefore document how episodic and cumulative disturbances impact the ecological integrity of an ecosystem while physical and chemical variables are snapshot and report problems taking place at the moment of sampling (Dale and Beyeler, 2001; Li et al., 2010; Siddig et al., 2016). As such, biological parameters are studied as more sensitive indicators of ecosystem integrity than physical and chemical parameters (Beyene et al., 2009; Siddig et al., 2016; Dalu et al., 2017).

Biological monitoring implies the systematic use of living organisms (biological indicators) or their responses to determine and monitor the condition or changes of the environment (Li et al., 2010; Lopez-Lopez and Sedeno-Diaz, 2015). Biological monitoring of freshwater ecosystems is acclaimed to be a quick and cost-effective method for assessing ecosystem conditions (Ollis et al. 2006; Dallas et al., 2010; Li et al., 2010; Lopez-Lopez and Sedeno-Diaz, 2015). It allows long-term environmental effects to be detected, providing a broad measure of their synergistic impacts (Dalu and Froneman, 2016). Such biological monitoring allows for better-informed and more cost-effective management decisions (Siddig et al., 2016).

A number of organisms (e.g., periphyton, benthic macroinvertebrates, fish, and macrophytes) have been used as biological indicators in the assessment of freshwater ecosystem conditions worldwide (Dallas, 1995; Resh et al., 1995; Barbour et al., 1999; Hering et al., 2006). In Europe, for example, the Water Framework Directive advocates the use of different organism groups to be used either singly or together in assessing the ecological integrity of inland waters and coastal regions (Council of the European Communities, 2000; Hering et al., 2006; Johnson et al., 2007). In many regions, benthic macroinvertebrates are most commonly used to monitor the ecological status of aquatic ecosystems (Dallas, 1995; Li et al., 2010; Aschalew and Moog, 2015; Siddig et al., 2016; Nhiwatiwa et al., 2017), including temporary wetlands (Van den Broeck et al., 2015) . This is because they are ubiquitous and most abundant even in small water bodies, are taxonomically rich, and form key integral components of aquatic food webs (Rosenberg and Resh, 1993; Barbour et al., 1999; Ollis et al., 2006; Resh, 2008). Benthic macroinvertebrates are regarded as good indicator organisms because they show taxon-specific differences in sensitivity to pollution, and have an aquatic life span long enough to provide an integrated record of environmental quality (Metcalfe 1989; Barbour et al. 1999; Nhiwatiwa et al., 2017). Bioassessment methods based on macroinvertebrates range from sub-organism (e.g., cell or tissue) to ecosystem-level, but community-level methods are most widely applied (Bonada et al., 2006; Kaaya, 2014).

In temporary wetland, a number of families or genera of macroinvertebrates have shown to be potential bio-indicators for fast and cost-effective monitoring of the overall ecosystem quality (Boix et al., 2005; Oertli et al., 2005; Sanchez-Fernandez et al., 2006; Van den Broeck et al., 2015). In temporary waters of southern England, water beetles (Coleoptera), for example, were found to be highly correlated with conductivity, turbidity and pool depth (Gutiérrez-estrada and Bilton, 2010). Dragonfly and damselfly (Odonata) larvae have also shown to be good biological indicators of grazing impacts (Foote and Hornung, 2005; Silver and Vamosi, 2012). The dipterans such as *Ochlerotatus/Aedes*, *Cricotopus*, *Thienemanniella*, *Synorthocladius* and *Tvetenia* are known to be good indicators for highly disturbed temporary wetlands (Trigal et al., 2007; Lysyk, 2010; Schneider et al., 2012). Other potential bio-indicators in the temporary aquatic habitats are the large branchiopods (Anostraca, Notostraca, Laevicaudata, Spinicaudata and Cyclestherida), which are often considered to be the flagship group of these habitats (Brendonck et al., 2008; Van den Broeck et al., 2015). Several studies have indicated that large branchiopods are sensitive to stressors, including habitat modification (Vanschoenwinkel et al., 2013), climate and hydrological changes (Pyke, 2005; Tuytens et al., 2014), salinity (Waterkeyn et al., 2010; Mabidi et al., 2018), and pollution (Hamer and Brendonck, 1997).

In Tanzania, the use of biological indicators to assess river and wetland quality is limited, with application focusing on benthic macroinvertebrate assemblages in river systems being established albeit relatively recently (Elias et al., 2014; Kaaya et al., 2015) and not commonly performed (Shimba and Jonah, 2016). Thus far, only a few studies on benthic macroinvertebrates have been published (e.g., Elias et al., 2014; Kaaya et al., 2015; Shimba and Jonah, 2016; Masikini et al., 2018). Notably, these studies were conducted only as a part of basic scientific research as no regulations or laws in Tanzania stipulate the use of biological indicators for measuring water quality to meet governmental regulations.

6. Tanzania River Scoring System (TARISS): A macroinvertebrate biotic index for rapid bioassessment of rivers

Rapid bioassessment methods (RBMs) of rivers and streams are techniques used for the assessment of general river conditions or health as influenced by a variety of factors but principally water quality (Barbour et al., 1999; Dickens and Graham, 2002; Kaaya et al., 2015). RBMs are a practical technical approach for conducting cost-effective, yet scientifically valid, procedures for biological monitoring of river systems (Barbour et al., 1999). As such, there has been a proliferation of techniques used for the rapid bioassessment of rivers around the world e.g., the River Invertebrate Prediction and Classification System (RIVPACS) in the United Kingdom (Wright et al., 1984), the Australian River Assessment System (AUSRIVAS) in Australia (Davies, 2000), the South African Scoring System (SASS) in South Africa (Dickens and Graham, 2002) and the Namibian Scoring System (NASS) in Namibia (Palmer and Taylor, 2004). The widespread use of RBMs has been promoted by regulatory authorities who see the value of bioassessment information for the management of water resources (Barbour et al., 1999; Dickens and Graham, 2002; Kaaya et al., 2015).

In Tanzania, a biotic index based on aquatic macroinvertebrates (i.e., the Tanzania River Scoring System (TARISS) for assessing the ecological conditions of river systems has been recently developed (Kaaya et al., 2015). TARISS has been adapted from SASS5 which is broadly used in South Africa where it forms the backbone of the National River Health Program (Dallas, 1997; Dickens and Graham, 2002; Dallas et al., 2010). Modification of TARISS was based on the assumption that SASS macroinvertebrate sensitivity weightings are appropriate reflections of pollution and general disturbance in river condition. Sensitivity weightings for the new taxa (specific Tanzania taxa) were derived based on the SASS macroinvertebrate sensitivity weightings scale (1-15) (Kaaya, 2014). TARISS has been recommended for the assessment of the ecological conditions of river systems in Tanzania and the East-Africa region (Kaaya, 2014). However, it needs to be tested, validated and modified (where necessary) before its full application. This is because differences in climate, geology, longitude and latitude between river basins and regions may contribute to differences in the physical and chemical characteristics of rivers, resulting in variations in macroinvertebrate assemblages and sensitivity levels in relation to disturbance and general ecosystem impairment. Thus far, TARISS has not been extensively tested in river systems in Tanzania, but was applied in Uganda (Tumusiime et al., 2019) and Rwanda (Dusabe et al., 2019) with some modifications and it was concluded that the TARISS score was able to distinguish between test and reference sites.

Following the TARISS protocol, macroinvertebrates are sampled by using a kick net of 1 mm mesh size on a 30 x 30 cm^2 frame. Samples are collected separately in three biotopes, namely stones, vegetation/macrophytes and gravel sand mud (GSM) biotopes (Kaaya et al., 2015). The stone biotope comprises samples collected from stones in current (SIC) and out of current (SOOC). In sampling, stones are kicked, scraped, turned or rubbed with hands and feet while the disturbed area is continuously being swept by the net for a period of one to five minutes. The vegetation biotope includes marginal and aquatic vegetation. Marginal vegetation refers to vegetation on the edge of riverbanks and aquatic vegetation refers to submerged vegetation in the river channel, including filamentous algae and roots and stems of floating vegetation. For sampling of aquatic vegetation, a net is repeatedly pushed through the submerged or floating aquatic vegetation over an area of approximately one square meter. For marginal vegetation, a length of approximately two meters of marginal vegetation is sampled covering both reeds, shrubs and grasses and different flow velocities (i.e., fast and slow) (Kaaya, 2014). For GSM biotopes, samples are collected from gravel (2-16 mm), sand (0.06-2mm) and mud, silt or clay (<0.06mm) in different available water currents for one minute. GSM biotopes are stirred by shuffling one’s feet while the shuffled area is continuously swept over by a net to catch dislodged organisms. Sampling times mentioned for each biotope refer to the actual sampling time (kicking, stirring or sweeping) excluding the time spent crossing the river (Kaaya, 2014).

Identification of macroinvertebrate taxa is done up to the family level for most taxa except for the Phyla Coelenterata (Cnidaria) and Porifera (Sponges), and classes Oligochaeta, Hirudinea and Turbellaria. Three metrics are calculated for TARISS: Number of Taxa, TARISS Score and ASPT. The calculation of results is done by ticking any families observed (irrespective of abundance), in any of the biotopes (stone, vegetation and GSM), in the combined column (C) of the scoring sheet. Sensitivity weightings for each taxon ticked in the combined column are summed to provide the TARISS Score. The total number of taxa found is counted and recorded as number of taxa. The TARISS score is divided by the Number of Taxa, to provide the ASPT. Sensitivity weightings range between 1 and 15: low sensitivity (1-5), moderate (6-10) and high sensitivity (11-15). A sliding scale for the identification of Baetidae and Hydopsychidae families is used because these families are represented by a wide range of species. The sliding scale operates under the assumption that the more species are available at a site the less disturbed the site is, such that a sensitivity weighting of 4 is given to Baetidae 1sp, 6 to Baetidae 2sp and 12 to Baetidae > 2sp (Kaaya, 2014). TARISS is designed for use in perennial lotic systems of low to moderate hydrological flows, and not intended for use in wetlands, impoundments, estuaries and other lentic systems (Kaaya et al., 2015).

7. Description of the study area

The Upper Pangani River Basin (UPRB) (~13400 km^2) is a trans-boundary river basin shared by Kenya (5% of basin) and Tanzania (95% of basin) in Eastern Africa. The study area covers the Tanzanian part of the basin in northeastern of Tanzania (Fig.7). The basin derives its main water sources from perennial springs along the slopes of Mt. Meru (4,565 m.a.s.l.) and Mt. Kilimanjaro (5,895 m.a.s.l.). The Upper Pangani River Basin has a semi-arid climate, with an annual mean temperature of 21°C and average annual precipitation of approximately 2500 mm in the highlands and around 500 mm in the lowland (NSCA, 2007; PBWO/IUCN, 2007a). The basin experiences two rainy seasons: the long rains (*masika*) from March through May and the short rains (*vuli*) which are less reliable and normally coming in November and December; the dry season (*kiangazi*) is from June to October (Kiptala et al., 2013).

UPRB is of high socio-economic importance to the local communities in Arusha, Manyara and Kilimanjaro regions (Turpie et al., 2005), and of ecological importance to the region (PBWO/IUCN, 2007b). The river provides multiple direct and indirect ecosystem services such as a source of drinking water (both for human and livestock), food (e.g., fish), and hydroelectric power (from Nyumba ya Mungu reservoir/dam). Mbonile (2005) and PBWO/IUCN (2007b) reported higher population density in the upper Pangani River Basin because of more favorable living conditions and the availability of fertile soils for agriculture, in particular. The basin has experienced increasing human population growth (Mbonile 2006; Shaghude 2006, PBWO/IUCN 2007b), with an average population increase of 20% (2002 to 2012) (National Bureau of Statistics 2013) and an annual population growth rate estimated at 2.7% (Arusha), 1.8 % (Kilimanjaro) and 3.2% (Manyara) (National Bureau of Statistics 2013). Owing to this population growth and the concurrent increase in food demand and urbanization, a substantial amount of natural forest land has been converted to settlement and/or agriculture land. Subsequently, this has resulted in the intensification of agriculture activities and over-abstraction of water for irrigation, amounting to about 80% of the total water use (PBWO/IUCN 2007b). The basin is also an important biodiversity hotspot: the national parks (including Arusha National park and Kilimanjaro National park), the Eastern Arc mountains, extensive forests and freshwater habitats (lakes, rivers, and wetlands) make an outstanding reservoir of plant and animal species (PBWO/IUCN, 2007b; URT, 2014).

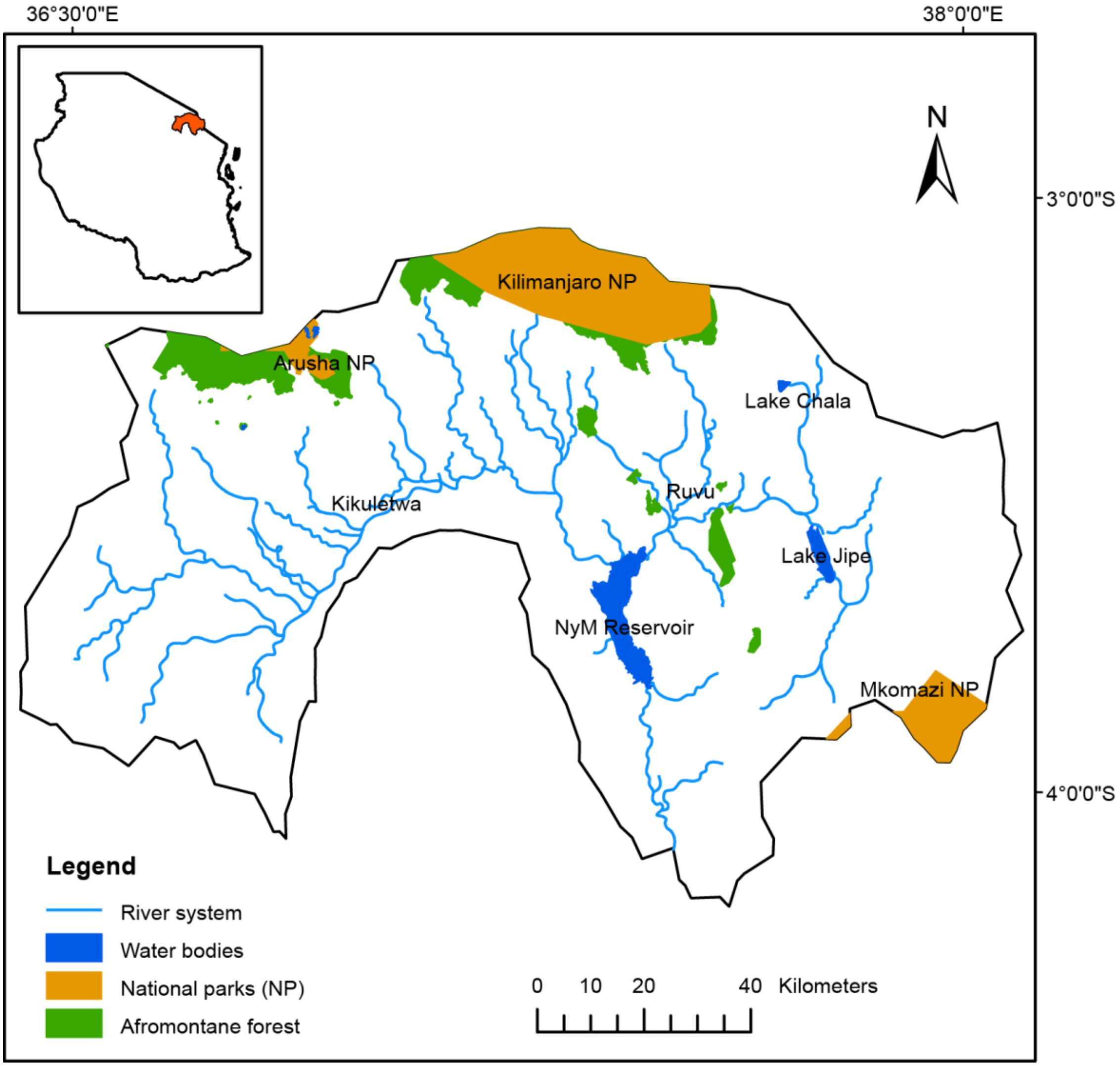


Fig.7. Map of the Upper Pangani River Basin (UPRB) showing the river network and available water bodies. Insert: Map of Tanzania with the location of the UPRB.

Landuse in the catchment is highly influenced by the three distinct agro-ecological zones based on soils, altitude, and climate. The zones include the peaks of Mt. Kilimanjaro and Mt.Meru (1,800 to 5,895 m.a.s.l.), the highlands (1000 to 1,800 meters a.s.l) and the lowland /plains (below 1000 meters a.s.l.) (UNDP 2014). The highland zone has relatively fertile soils and consists of an Afrotropical montane rain forest (along the Mt. Kilimanjaro and Mt. Meru forest reserve), and multi-strata agroforestry (with intercropped coffee and banana plantations as main crops). Other crops include maize, round potato, yams, vegetables, and fodder cultivation which are grown in small plots. Livestock keeping includes dairy cattle, dairy goats, pigs, and sheep which is done through zero-grazing (Mathew et al. 2016). The middle and lowland plains consist of savanna bushland, small and large-scale irrigated agriculture, shrub-land and grassland, herding, fishing, and small industries. Common crops grown in this zone include; rice, maize, beans, millet, cowpeas, cotton, sisal, sugarcane, sunflower, sorghum, pigeon peas, cassava, green gram, fruits (e.g. watermelon), and vegetables (such as onions, cucumber, green pepper, tomatoes, and eggplants) (Kiptala et al., 2013; UNDP, 2014; Mathew et al., 2016). Irrigation is highly practiced in this zone using both surface water (rivers and streams) and groundwater. Livestock keeping is a mixture of staff-fed and free livestock grazing, with mainly indigenous breeds of cows (Kilimanjaro Zebu), goats and sheep (Mathew et al. 2016)

As a major economic activity in the basin, agriculture goes hand in hand with the application of fertilizers to improve the agricultural yield. According to the International Fertilizer Development Centre (2012), the use of fertilizers in Tanzania has increased from 120 x 10^3 metric tons in 2005/06 to 263 x10^3 metric tons in 2009/10, and the application levels are likely to increase in future due to agricultural sector development. The Kilimanjaro and Arusha regions are among the major fertilizer consuming regions in the northern part of Tanzania (International Fertilizer Development Centre 2012). According to TNSCA (2007), about 65% of the annual crop cultivated land in the Kilimanjaro and Arusha regions is under fertilizer application, both inorganic and organic fertilizer (farmyard manure). The inorganic fertilizers include CAN: Calcium Ammonium Nitrate ($NH4NO_3 + CaCO_3 * MgCO_3$), Urea ($CH_4N_2O$), NPK, DAP: Di-ammonium Phosphate ($(NH4)_2HPO_4$), and SA: Ammonium Sulphate ($(NH4)_2\ SO_4$). Urea and DAP account for about 50 percent of the total fertilizer use (International Fertilizer Development Centre 2012). The study of Kihampa et al. (2013) indicated that fertilizer application in the agricultural fields in the Pangani basin is probably one of the diffuse sources of nutrients (nitrogen compounds and phosphate) causing pollution (eutrophication) of surface water resources.

The UPRB is considered water-stressed with some of its tributaries only flowing for part of the year (PBWO/IUCN, 2007a; Komakech and Zaag, 2011). Over-abstraction of water for irrigation purposes is considered as one of the main factors attributing to water stress in the basin (Shaghude, 2006; PBWO/IUCN, 2007a; Komakech and Zaag, 2011; Lalika et al., 2015b). Two types of irrigation systems have evolved in the basin i.e., the large-scale irrigation systems and small-scale traditional irrigation (furrow) systems (Shaghude, 2006). Large-scale commercial irrigation utilize large quantities of water owing to large farm sizes and farming of water-intensive crops such as rice paddies, sugarcane, and flowers (Turpie et al., 2005; Shaghude, 2006; PBWO/IUCN, 2007a; Komakech, 2013). The traditional irrigation systems date back to pre-colonial times where irrigation is facilitated through an extensive furrow network. At present over 2,000 furrow systems are reported to be active in the basin (Shaghude, 2006; Komakech and Zaag, 2011). The furrow systems are very inefficient with significant water wastage of up to 85%, mainly through leakage and evaporation (IUCN, 2009; Komakech, 2013). The irrigation abstraction systems (large-scale and traditional) are estimated to use at least 400 million m^3 per annum (Shaghude, 2006). Changes directly linked with the excessive abstraction of water are the modifications of streamflow in many parts of the UPRB, including the Kikuletwa River. Studies on the Kikuletwa River show the reduced trends in the dry season flows, with the lower section of the river only flowing in the wet season, suggesting that the flow is associated with irrigation abstraction which largely occurs during dry seasons (Shaghude, 2006; IUCN, 2009; Komakech, 2013). The observed declining trend in water flow has adverse impacts on the environmental flow, ecological processes, and the overall provision of ecosystem services (Mwamila et al., 2008; Lalika et al., 2015b). PBWO/IUCN (2007b) observed poor water quality with high nutrient concentrations and low oxygen levels in the Kikuletwa River at Wahoga Chini in the dry season which was associated with a critical reduction in river flow. Mwamila et al. (2008) found that the reduction in high-flow occurrences has great negative impacts on fish spawning, growth, and the overall fish productivity in the Kirua swamps.

The UPRB is managed by the Ministry of Water under the Pangani Basin Water Board (PBWB) and the Pangani Basin Water Office (PBWO). The Water Utilization (Control and Regulation) Act No. 42, 1974 of Tanzania was amended in 1981 (Amendment Act No. 10) to delegate the responsibility for water management at the level of the basin of nine rivers, including Pangani River Basin (The Water Utilization Control and Regulation Amendment Act, 1981). In 1991, the PBWO was subsequently established to manage and regulate the uses of water in the basin (both in terms of quality and quantity), guided by PBWB. The PBWO and PBWB are responsible for: (i) water resource assessment, (ii) allocating water for different uses (issuing and management of water permits), (iii) managing and controlling water use, (iv) monitoring and controlling pollution, (v) water-related conflict resolution, (vi) awareness creation on effective and efficient water use (strengthen community participation in water resources management), (vii) collection of water use and wastewater discharge fees, and (viii) protection and conservation of water sources. However, watershed conservation and good water governance are among the present-day challenges in the basin (Komakech, 2013; Lalika et al., 2015a).

8. Study systems

The study was carried out in the Usa-Kikuletwa and Ruvu River catchments which are located in the UPRB (Fig.8 and Fig.9). The river systems are characterized by a latitudinal spatial range of land-use activities from upstream to downstream which make it possible to study natural and anthropogenic influences on the river systems (Fig.10).

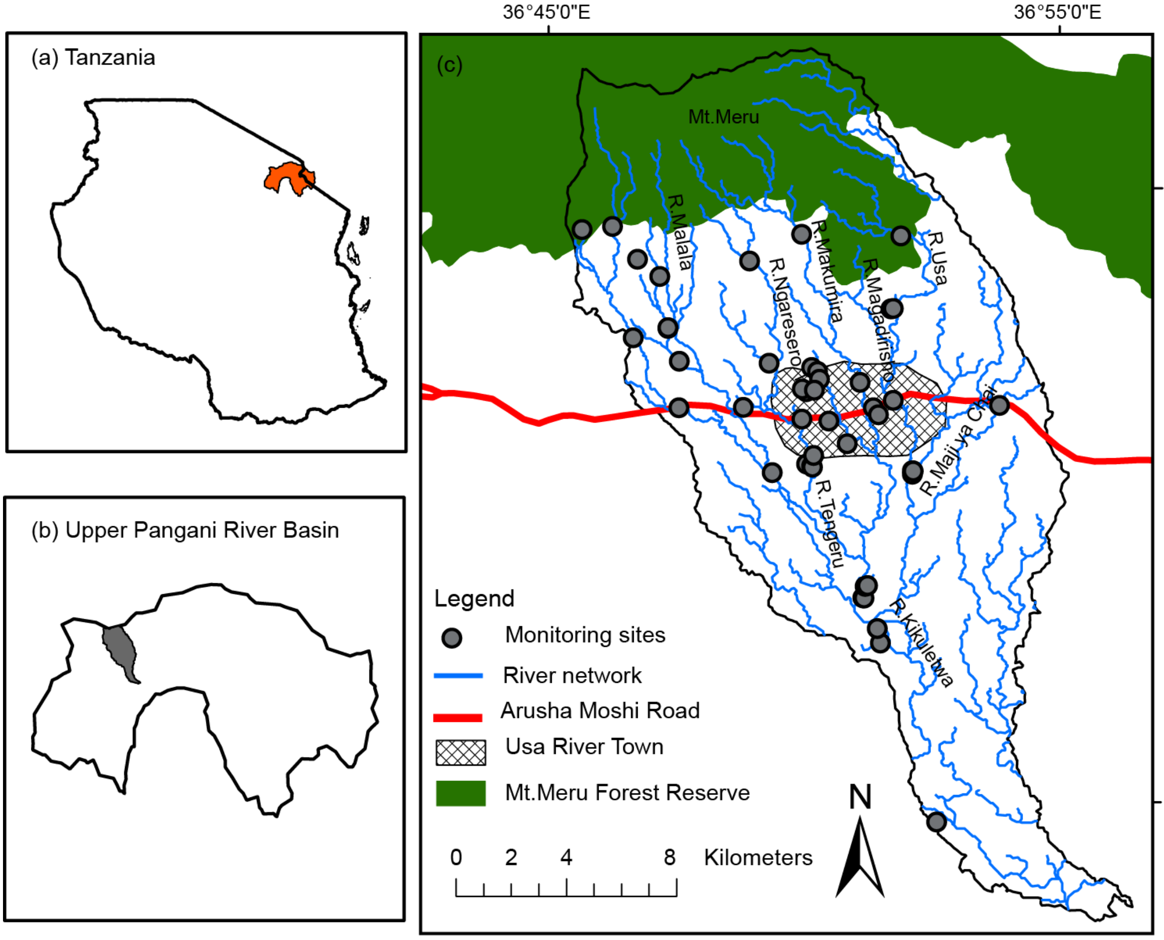


Fig.8. Map of the Usa-Kikuletwa River catchment in northeastern Tanzania showing the location of the monitoring sites. Inserts: (a) map of Tanzania with the location of the UPRB, and (b) map of UPRB with the location of the Usa-Kikuletwa River catchment.

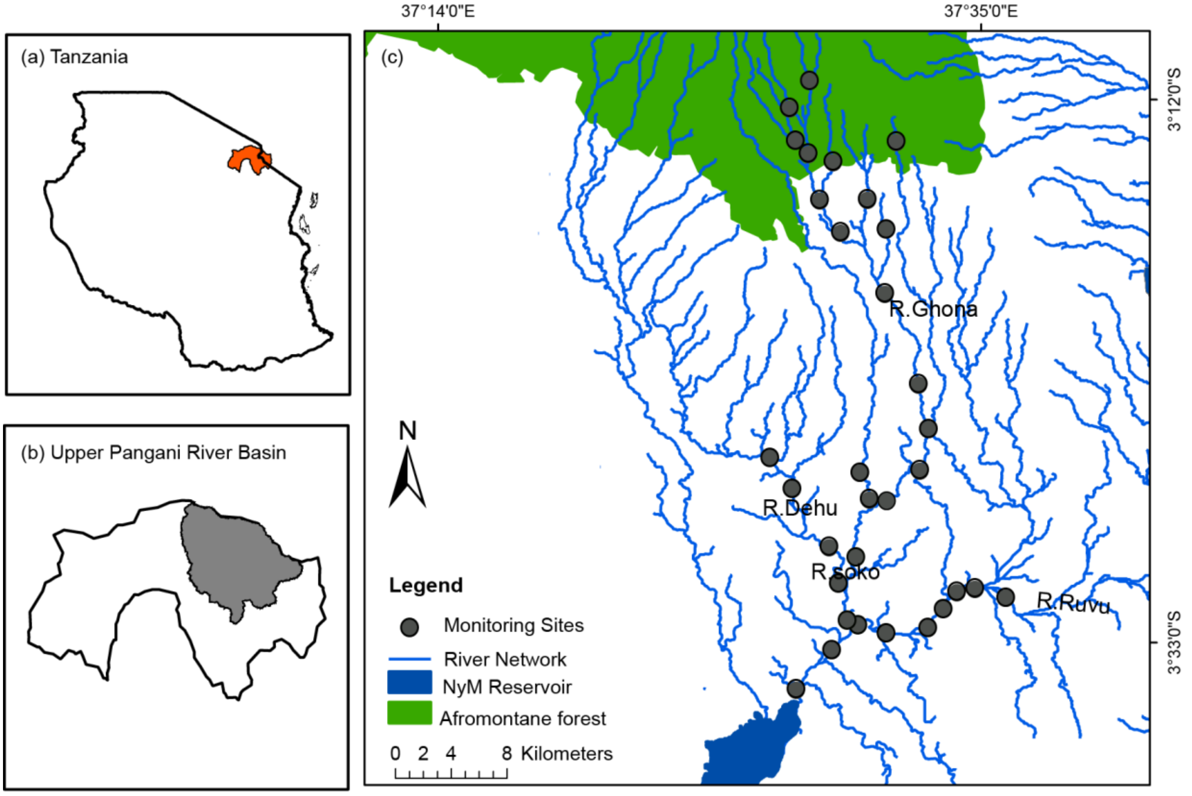


Fig.9. Map of the Ruvu River catchment in the northeastern Tanzania showing the location of the monitoring sites. Inserts: (a) map of Tanzania with the location of the UPRB, and (b) map of UPRB with the location of the Ruvu River catchment.

Fig.10. Pictures of river sections in the upper reaches (top row), middle reaches (middle row) and lower reaches (bottom row) of the Ruvu River catchment (left column) and Usa-kikuletwa River catchment (right column). Photographs by Grite N Mwaijengo and Emilie Hermans.

Besides rivers and streams, the alluvial floodplain of the Ruvu River catchment comprises a mosaic of temporary pool ecosystems (Fig.11). They include a group of isolated endorheic pools that are only rain-filled, and a group of river-connected pools that are also rain-filled but seasonally connect to the river channel during flooding (Fig.12). All temporary pools (i.e., endorheic and river connected pools) start to fill up at the start of the rainy season (March) and dry up in the dry season (from June to February). However, the timing and duration of filling episodes vary substantially between years, depending on the rainfall patterns. Some pools can remain inundated through to May, however, small endorheic pools are short-lived and dry-up within four weeks. Later, at the peak of the rainy season (April), river connected pools connect with the Ruvu River (i.e., when the river floods the flanking plains). The connectivity can last for few days to about two weeks depending on the rainfall intensity. Generally, flooding of the Ruvu River occurs once a year at the peak of the rainy season (April), except for dry years when the amount of rainfall is relatively low and subsequently the water level in the Ruvu River become extremely low. The seasonal flooding of Ruvu River maintains the hydrological connectivity between the river channel and the floodplain pools and govern many of the floodplain habitat characteristics including biodiversity, environmental conditions and pattern of land-use by communities living adjacent to the river-floodplain ecosystem.

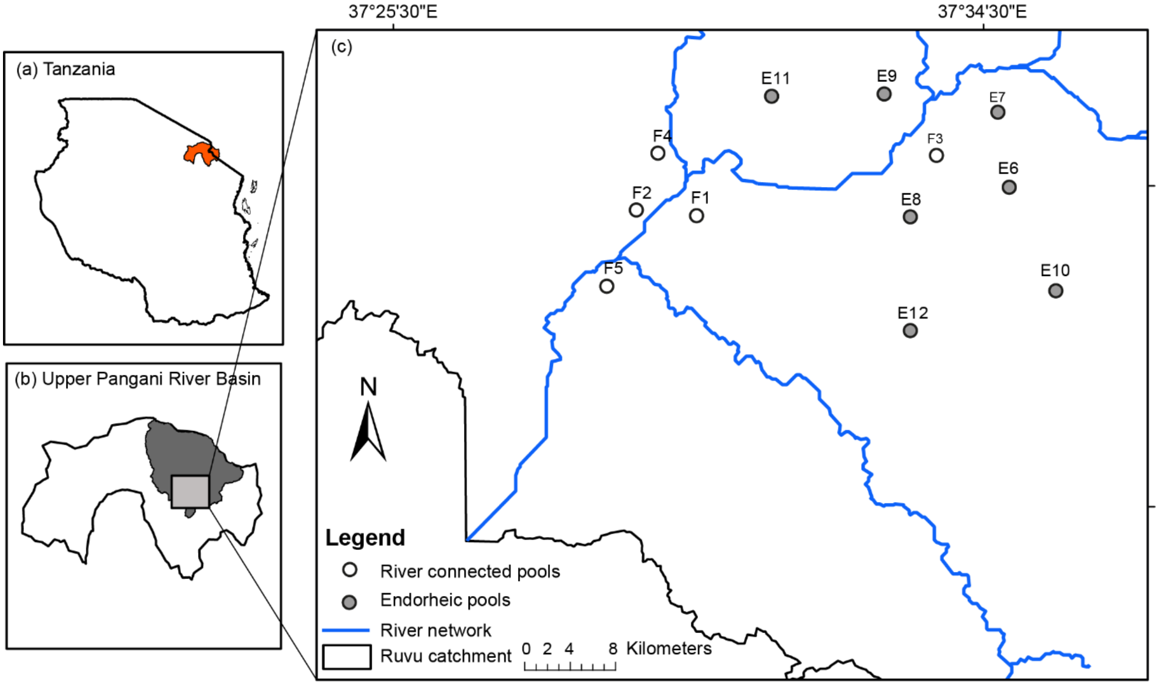


Fig.11. Geographical location of temporary pools (endorheic pools = filled circles; floodplain pools = empty circles) in the Ruvu River catchment, northeastern Tanzania. Inserts: (a) map of Tanzania with the location of the UPRB, and (b) map of UPRB with the location of Ruvu River catchment.

Fig.12. Pictures of endorheic wetlands (top row) and floodplain wetlands (bottom row) in the Ruvu River catchment.

9. Outline of the thesis

The main goal of the thesis is to investigate different factors that can explain biodiversity and ecosystem quality in tropical river systems and associated temporary pool ecosystems in the north-eastern part of Tanzania. In general, three main research objectives are addressed: (i) to assess how aquatic communities are influenced by seasonal variation in riverine conditions (Chapters 1, 2 and 4), (ii) to assess the impact of land-use and spatial scale on river quality (Chapters 1 and 2), and (iii) to evaluate how connectivity (i.e., longitudinal hydrological connectivity (spatial stream networks) and lateral hydrological connectivity) modulate physical, chemical and biological processes in river and floodplain habitats (Chapters 3 and 4). We tackle these goals using a step by step approach starting from describing variation in riverine communities and water quality in the dry and wet season. Subsequently, we identify indicator taxa for the different water quality conditions in different seasons **(Chapter 1)**. Using this information, we then explore to what extent land-use is responsible for these patterns. To do this we scrutinize a set of different procedures that can be used to define relevant land-use for different river sites **(Chapter 2).** In **Chapter 3** we add a main constraint that is not always included in studies of river systems: connectivity and spatial autocorrelation of sites. For this we use a spatially explicit analysis framework to test to what extent spatial stream networks (connectivity) affects differences in biodiversity and water quality in a river system. Finally, we assess to what extent seasonal connectivity of the river with temporary wetlands in the surrounding landscape is a crucial determinant of water quality and communities in these wetlands. This was achieved by comparing environmental conditions and aquatic communities from river connected pools with endorheic pools **(Chapter 4)**. With this knowledge we contribute to important baseline information on the status of these ecosystems in the region. In addition, we develop a number of novel insights in the ecology of these systems and their interactions in a landscape context. In the general discussion, we synthesize the main findings and suggest the monitoring and conservation plans of these ecosystems in the region. The contents of each chapter and their mutual relationships is depicted in a graphical abstract (Fig.13).

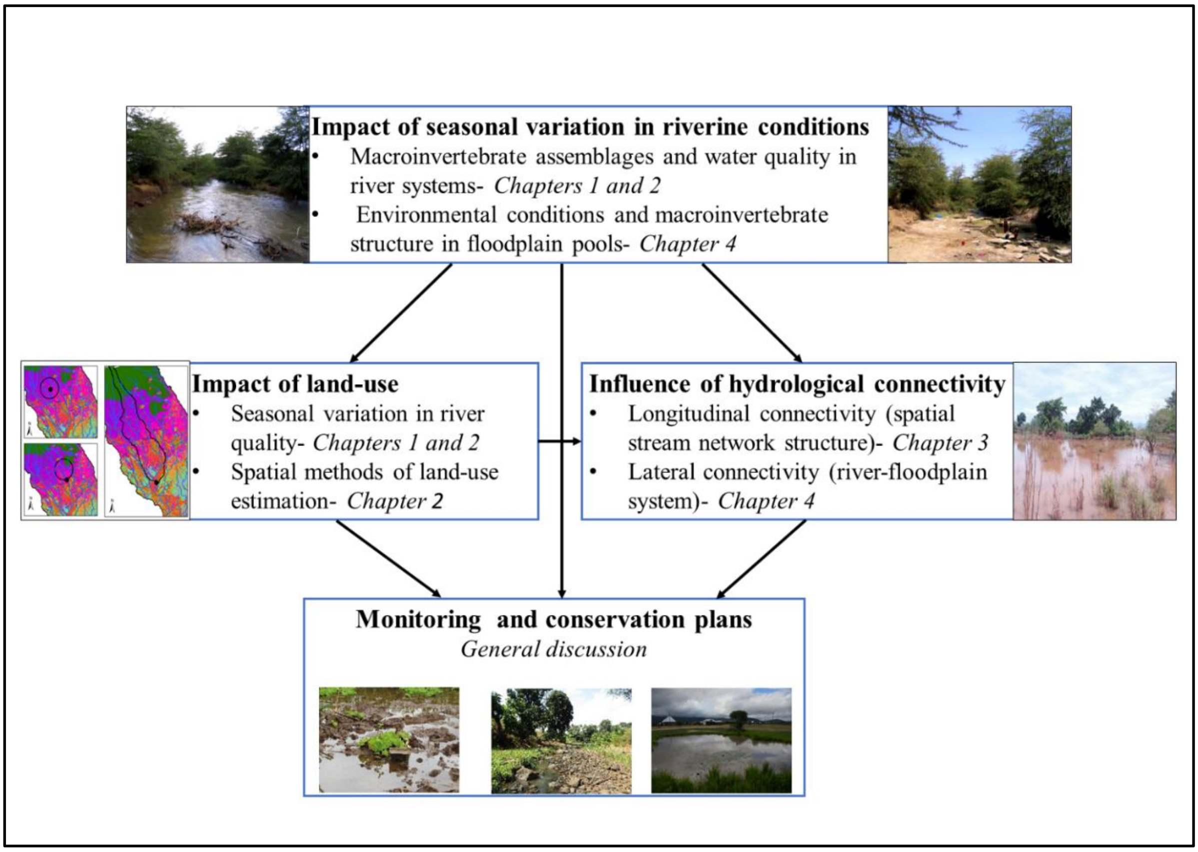


Fig. 13. Schematic overview of the thesis outline. The thesis contains three main sections with different main topics which interact throughout the thesis: Part one (Chapters 1, 2 and 4) focusses on the influence of seasonality on river-floodplain ecosystem functioning. Part two (Chapters 1 and 2) is focusing on the impact of land-use and spatial scale on river quality. Part three (Chapters 3 and 4) focusses on the importance of connectivity (i.e., longitudinal and lateral hydrological connectivity) in modulating physical, chemical and biological processes in river and floodplain habitats.

References

Allan, D.J., Castillo, M.M., 2007. Stream Ecology: Structure and Functioning of Running Waters, Second Edi. ed. Springer Netherlands.

Allan, D.J., Erickson, D.L., Fay, J., 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshw. Biol. 37, 149–161.

Allan, D.J., Russek, E., 1985. The Quantification of Stream Drift. Can. J. Fish. Aquat. Sci. 42, 210–215.

Allan, J.D., 2004. Landscapes and Riverscapes : The Influence of Land Use on Stream Ecosystems. Annu.Rev.Ecol.Syst 35, 257–84.

Allan, J.D., Flecker, A.S., 1993. Biodiversity Conservation in Running Waters Identifying the major factors that threaten destruction of. Bioscience 43, 32–43.

Allen, G.H., Pavelsky, T.M., 2018. Global extent of rivers and streams. Science (80-.). 361, 585–588.

Allen, T.F.H., Starr, T.B., 1982. Hierarchy: Perspectives for ecological complexity, Chicago: University of Chicago Press. Chicago.

Amoros, C., Bornette, G., 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshw. Biol. 47, 761–776.

Baptista, D.F., Dorvillé, L.F.M., Buss, D.F., Nessiamian, J.L., 2001. Spatial and temporal organization of aquatic insect assemblages in the longitudinal gradient of a tropical river. Brazilian J. Biol. 61, 295–304.

Barbero, M.D., Oberto, A.M., Gualdoni, C.M., 2013. Spatial and temporal patterns of macroinvertebrates in drift and on substrate of a mountain stream (Cordoba , Central Argentina). Acta Limnol. Bras. 25, 375–386.

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid Bioassessment Protocols For Use in Streams and Wadeable RiversWadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish. Second Ed. EPA 841-B-99-002. U.S. Environ. Prot. Agency; Off. Water; Washington, DC, USA. Brewin.

Beyene, A., Addis, T., Kifle, D., Legesse, W., Kloos, H., Triest, L., 2009. Comparative study of diatoms and macroinvertebrates as indicators of severe water pollution: Case study of the Kebena and Akaki rivers in Addis Ababa, Ethiopia. Ecol. Indic. 9, 381–392.

Boix, D., Gascon, S., Sala, J., Martinoy, M., Gifre, J., Quintana, X.D., 2005. A new index of water quality assessment in Mediterranean wetlands based on crustacean and insect assemblages : the case of Catalunya (NE Iberian peninsula). Aquat. Conserv. Mar. Freshw. Ecosyetems 15, 635–651.

Boix, D., Kneitel, J., Robson, B.J., Duchet, C., Zúñiga, L., Day, J., Gascón, S., Sala, J., Quintana, X.D., Leon, B., 2016. Invertebrates of temporary Ponds in Mediterranean Climates. In: Batzer, D. & Boix, D. (eds.) Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology. Cham: Springer International Publishing, pp. 645, 141-189.

Boix, D., Sala, J., Gascon, S., Brucet, S., 2006. Predation in a temporary pond with special attention to the trophic role of Triops cancriformis (Crustacea : Branchiopoda : Notostraca) Predation in a temporary pond with special attention to the trophic role of Triops cancriformis (Crustacea : Branchi. Hydrobiologia 571, 341–353.

Bonada, N., Prat, N., Resh, V.H., Statzner, B., 2006. Developments in Aquatic Insect Biomonitoring: A Comparative Analysis of Recent Approaches. Annu. Rev. Entomol. 51, 495–523.

Boulton, A.J., Boyero, L., Covich, A.P., Dobson, M., Lake, S., Pearson, R., 2008. Are Tropical Streams Ecologically Different from Temperate Streams?, in: Tropical Stream Ecology. pp. 257–284.

Boven, L., Brendonck, L., 2009. Impact of hydroperiod on seasonal dynamics in temporary pool cladoceran communities. Fundam. Appl. Limnol. Arch. für Hydrobiol. 174, 147–157.

Boyero, L., 2002. Insect biodiversity in freshwater ecosystems: is there any latitudinal gradient? Mar. Freshw. Res. 53, 753–755.

Boyero, L., Bosch, J., 2002. Spatial and Temporal Variation of Macroinvertebrate Drift in Two Neotropical Streams. Biotropica 34, 567–574.

Boyero, L., Ramirez, A., Dudgeon, D., Pearson, R.G., 2009. Are tropical streams really different ? J. North Am. Benthol. Soc. 28, 397–403.

Brendonck, L., De Meester, L., 2003. Egg banks in freshwater zooplankton : evolutionary and ecological. Hydrobiologia 491, 65–84.

Brendonck, L., Michels, E., De Meester, L., Riddoch, B., 2002. Temporary pools are not “enemy-free”.In: Maeda-Martinez, A.M., B.V. Timms, D.C. Rogers, F.A. Abreu-Grobois & G. Murugan (Eds), Studies on Large Branchiopod Biology 4. Hydrobiologia 486: 147-159.

Brendonck, L., Rogers, C.D., Olesen, J., Weeks, S., Hoeh, W.R., 2008. Global diversity of large branchiopods (Crustacea : Branchiopoda) in freshwater. Hydrobiologia 595, 167–176.

Brendonck, L., Williams, W.D., 2000. Biodiversity in wetlands of dry regions (drylands) In: Biodiversity in wetlands: assessment, function and conservation vol. 1. Gopal, B., W.J. Junk & J.A. Davis (Editors). Backhuys Publishers, Leiden, The Netherlands, pp. 181-194.

Brittain, J.E., Eikeland, T.J., 1988. Invertebrate drift - A review. Hydrobiologia 166, 77–93.

Brooks, R.T., Hayashi, M., 2002. Depth-Area-Volume and Hdroperiod Relationships of Ephemeral (Vernal) Forest Pools in Southern New England. Wetlands 22, 247–255.

Brown, B.L., Swan, C.M., 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. J. Anim. Ecol. 79, 571–580.

Bruns, D.A., Minshall, W.G., Cushing, C.E., Cummins, K.W., Brock, J. ames T., Vannote, R.L., 1984. Tributaries as modifiers of the river continuum concept: analysis by polar ordination and regression models. Arch. fur Hydrobiol. 99, 208–220.

Brussock, P.P., Brown, A. V, 1991. Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos. Hydrobiologia 220, 109–117.

Chen, H., Zhang, W., Gao, H., Nie, N., 2018. Climate Change and Anthropogenic Impacts on Wetland and Agriculture in the Songnen and Sanjiang Plain, Northeast China. Remote Sens. 10, 1–25.

Costanza, R., D’Arge, R., De Groot, R., Farber, S., Grassot, M., Hannon, B., Limburg, K., Naeem, S., Neilltt, R.V.O., Paruelo, J., Raskin, R.G., Sutton, P., Belt, M. Van Den, 1997. The value of the world’s ecosystem services and natural capital. Nature 387, 253–260.

Council of the European Communities, 2000. Establishing a Framework for Community Action in the field of Water Policy. Directive 2000/60/EC.

Cowell, B.C., Carew, W.C., 1976. Seasonal and diel periodicity in the drift of aquatic insects in a subtropical Florida stream. Freshw. Biol. 6, 587–594.

Cummins, K.W., Merritt, R.W., Andrade, P.C.N., 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. Stud. Neotrop.

Fauna Environ. 40, 69–89.

Cushing, C.., McIntire, C.., Cummins, K.., Minshall, G.., Petersen, R.C., Sedell, B.R., Vannote, R, L., 1983. Relationships among chemical, physical, and biological indices along river continua based on multivariate analyses. Arch. fur Hydrobiol. 98, 317–326.

Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. Ecol. Indic. 1, 3–10.

Dallas, H., Kennedy, M., Taylor, J., Lowe, S., Murphy, K., 2010. SAFRASS : Southern African River Assessment Scheme WP4 : Review of existing biomonitoring methodologies and appropriateness for adaptation to river quality assessment protocols for use in southern tropical Africa.

Dallas, H.F., 2004. Seasonal variability of macroinvertebrate assemblages in two regions of South Africa : implications for aquatic bioassessment. African J. Aquat. Sci. 29, 173–184.

Dallas, H.F., 1997. A Preliminary Evaluation of Aspects of SASS (South African Scoring System) for the Rapid Bioassessment of Water Quality in Rivers , With Particular Reference to the Incorporation of SASS in a National Biomonitoring Programme. South. African J. Aquat. Sci. 23, 37–41.

Dallas, H.F., 1995. An Evaluation of SASS (South African Scoring System) as a Tool for the Rapid Bioassessment of Water Quality. University of Cape Town (UCT), South Africa.

Dalu, T., Froneman, W.P., 2016. Diatom-based water quality monitoring in southern Africa : challenges and future prospects. Water SA 42, 551–559.

Dalu, T., Wasserman, R.J., Magoro, M.L., Mwedzi, T., Froneman, W.P., Weyl, O.L.F., 2017. Variation partitioning of benthic diatom community matrices : Effects of multiple variables on benthic diatom communities in an Austral temperate river system. Sci. Total Environ. 601-602, 73–82.

Davies, P.., 2000. Development of a national bioassessment system (AUSRIVAS) in Australia, in: Wright JF, Sutcliffe DWand Furse MT (eds.), Assessing the Biological Quality of Freshwaters. RIVPACS and Other Techniques. Freshwater Biological Association, Ambleside. pp. 113–124.

Davies, P.M., Bunn, S.E., Hamilton, S.K., 2008. Primary Production in Tropical Streams and Rivers, in: Tropical Stream Ecology. pp. 23–42.

De Meester, L., Declerck, S., Robby, S., Louette, G., Van De Meutter, F., De Bie, T., Michels, E., Brendonck, L., 2005. Ponds and pools as model systems in conservation biology , ecology and evolutionary biology. Aquat. Conserv. Mar. Freshw. Ecosyetems 15, 715–725.

Decamps, H., Naiman, R.J., 1990. Towards an ecotone perspective. Pp. 1–5 in Naiman, R.J.; Decamps, H. (Eds): Ecology and management of aquatic-terrestrial ecotones UNESCO Paris, and Parthenon Publishing Group, Camforth, UK.

Dickens, C.W., Graham, P.M., 2002. The South African Scoring System (SASS) Version 5 Rapid Bioassessment Method for Rivers. African J. Aquat. Sci. 27, 1–10.

Dobson, M., Magana, A., Mathooko, J.M., Ndegwa, F.K., 2002. Detritivores in Kenyan highland streams : more evidence for the paucity of shredders in the tropics ? Freshw. Biol. 47, 909–919.

Douglas, M.M., Bunn, S.E., Davies, P.M., 2005. River and wetland food webs in Australia ' s wet – dry tropics : general principles and implications for management. Mar. Freshw. Res. 56, 329–342.

Dube, T., Pinceel, T., Necker, L. De, Wepener, V., Lemmens, P., Brendonck, L., 2019. Lateral hydrological connectivity differentially affects the community characteristics of multiple groups of aquatic invertebrates in tropical wetland pans in South Africa. Freshw. Biol. 1–15.

Dudgeon, D., 2012. The Ecology of Tropical Asian Rivers and Streams in Relation to Biodiversity Conservation. Annu. Rev. Ecol. Syst. 31, 239–263.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z., Naiman, R.J., Knowler, D.J., Leveque, C., Soto, D., Prieur-Richard, A.-H., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity : importance , threats , status and conservation challenges. Biol. Rev. 81, 163–182.

Dusabe, M.-C., Wronski, T., Gomes-Silva, G., Plath, M., Albrecht, C., Apio, A., 2019. Biological water quality assessment in the degraded Mutara rangelands , northeastern Rwanda. Environ. Monit. Assess. 191, 1–13.

Elias, J.D., Ijumba, J.N., Mgaya, Y.D., Mamboya, F.A., 2014. Study on Freshwater Macroinvertebrates of Some Tanzanian Rivers as a Basis for Developing Biomonitoring Index for Assessing Pollution in Tropical African Regions. J. Ecosyst.

Elliott, J.M., 1969. Periodicity in Invertebrate Drift and the Effect of Different Sampling Periods. Oikos 20, 524–528.

Fagan, W.F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83, 3243–3249.

Fisher, S.J., Brown, M.L., Willis, D.W., 2001. Temporal food web variability in an upper Missouri River backwater : energy origination points and transfer mechanisms. Ecol. Freshw. Fish 10, 154–167.

Foote, L.A., Hornung, christine L.R., 2005. Odonates as biological indicators of grazing effects on Canadian prairie wetlands. Ecol. Entomol. 30, 273–283.

Frieden, J.C., Peterson, E.E., Webb, J.A., Negus, P.M., 2014. Improving the predictive power of spatial statistical models of stream macroinvertebrates using weighted autocovariance functions. Environ. Model. Softw. 60, 320–330.

Frissell, C.A., Liss, W.J., Warren, C.E., Hurley, M.D., 1986. A Hierarchical Framework for Stream Habitat Classification : Viewing Streams in a Watershed Context. Environ. Manage. 10, 199–214.

Gallardo, B., National, S., Paillex, A., 2014. Response of benthic macroinvertebrates to gradients in hydrological connectivity : a comparison of temperate , subtropical , Mediterranean and semiarid river floodplains. Freshw. Biol. 59, 630–648.

Ganio, L.M., Torgersen, C.E., Gresswell, R.E., 2005. A geostatistical approach for describing spatial pattern in stream networks. Front. Ecol. Environ. 3, 138–144.

Gibbins, C., Vericat, D., Batalla, R.J., 2007a. When is stream invertebrate drift catastrophic ? The role of hydraulics and sediment transport in initiating drift during flood events. Freshw. Biol. 52, 2369–2384.

Gibbins, C., Vericat, D., Batalla, R.J., Gomez, C.M., 2007b. Shaking and moving : low rates of sediment transport trigger mass drift of stream invertebrates. Can. J. Fish. Aquat. Sci. 64, 1–5.

Grant, E.H.C., Green, L.E., Lowe, W.H., 2009. Salamander occupancy in headwater stream networks. Freshw. Biol. 54, 1370–1378.

Grant, E.H.C., Lowe, W.H., Fagan, W.F., 2007. Living in the branches : population dynamics and ecological processes in dendritic networks. Ecol. Lett. 10, 165–175.

Gutiérrez-estrada, J.C., Bilton, D.T., 2010. A heuristic approach to predicting water beetle diversity in temporary and fluctuating waters. Ecol. Modell. 221, 1451–1462. h

Hamer, M.L., Brendonck, L., 1997. Distribution, diversity and conservation of Anostraca (Crustacea :Branchiopoda) in southern Africa. In: Simovich, M., Sassaman, C. & Belk, D. (eds.) Studies on Large Branchiopod Biology and Conservation. Springer Netherlands, 1, 1-12.

Hering, D., Johnson, R.K., Kramm, S., Schmutz, S., Szoszkiewicz, K., Verdonschot, P.F.M., 2006. Assessment of European streams with diatoms , macrophytes , macroinvertebrates and fish : a comparative metric-based analysis of organism response to stress. Freshw. Biol. 51, 1757–1785.

Humphries, P., Keckeis, H., Finlayson, B., 2014. The River Wave Concept : Integrating River Ecosystem Models. Bioscience 64, 870–882. https://doi.org/10.1093/biosci/biu130

International Fertilizer Development Centre, 2012. Tanzania fertilizer assessment report.Dar es Salaam, Tanzania

Isaak, D.J., Hoef, J.M. Ver, Peterson, E.E., Horan, D.L., Nagel, D.E., 2017. Scalable population estimates using spatial-stream-network (SSN) models , fish density surveys , and national geospatial database frameworks for streams. Can. J. Fish. Aquat. Sci. 74, 147–156.

Isaak, D.J., Peterson, E.E., VerHoef, J.M., Wenger, S.J., Falke, J.A., Torgersen, C.E., Sowder, C., Steel, A.E., Fortin, M., Jordan, C.E., Ruesch, A.S., Som, N., Monestiez, P., 2014. Applications of spatial statistical network models to stream data. WIREs Water 1, 277–294.

IUCN Eastern and Southern Africa Programme, 2009. The Pangani River Basin: A Situation Analysis, 2nd Edition.

Jackson, F.L., Fryer, R.J., Hannah, D.M., Millar, C.P., Malcolm, I.A., 2018. A spatio-temporal statistical model of maximum daily river temperatures to inform the management of Scotland ’ s Atlantic salmon rivers under climate change. Sci. Total Environ. 612, 1543–1558.

Jacobsen, D., 2008. Tropical High-Altitude Streams, in: Tropical Stream Ecology. pp. 219–256.

Jacobsen, D., Andino, P., Calvez, R., Cauvy-fraunié, S., Espinosa, R., Dangles, O., 2014. Temporal variability in discharge and benthic macroinvertebrate assemblages in a tropical glacier-fed stream. Freshw. Sci. 33, 32–45.

Johnson, B.L., Richardson, W.B., Naimo, T.J., 1995. Past, present, and future concepts in large river ecology: How rivers function and how human activities influence river processes. Bioscience 45, 134–141.

Junk, K.., Wantzen, W.., 2004. The Flood Pulse Concept: New Aspects, Approaches and Applications-An Update, in: Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, Food and Agriculture Organization of the United Nations (FAO) and the Mekong River Commission (MRC). pp. 117–140.

Junk, W.J., 1999. The flood pulse concept of large rivers : learning from the tropics. Large Rivers 11, 261–280.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989a. The Flood Pulse Concept in River-Floodplain Systems. Can. J. Fish. Aquat. Sci. 106, 110–127.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989b. The Flood Pulse Concept in River-Floodplain Systems, in: Dodge, D.P. (Ed.), Proceedings of the International Large River Symposium (LARS). Canadian Special Publication of Fisheries and Aquatic Sciences 106. pp. 110–127.

Kaaya, L.T., 2014. Biological Assessment of Tropical Riverine Systems Using Aquatic Macroinvertebrates in Tanzania, East Africa. University of Cape Town, South Africa.

Kaaya, L.T., Day, J.A., Dallas, H.F., 2015. Tanzania River Scoring System (TARISS): a macroinvertebrate-based biotic index for rapid bioassessment of rivers. African J. Aquat. Sci. 40, 109–117.

Kalkhoff, S.J., Hubbard, L.E., Tomer, M.D., James, D.E., 2016. Effect of variable annual precipitation and nutrient input on nitrogen and phosphorus transport from two Midwestern agricultural watersheds. Sci. Total Environ. 559, 53–62.

Keddy, P.A., 2010. Wetland Ecology: Principles and Conservation. Cambridge University Press, New York, pp. 497.

Kihampa, H.H., De Wael, K., Lugwisha, E., Van Grieken, R., 2013. Water quality assessment in the Pangani River basin, Tanzania: natural and anthropogenic influences on the concentrations of nutrients and inorganic ions. Int. J. River Basin Manag. 11, 55–75.

Kilonzo, F., Masese, F.O., Van Griensven, A., Bauwens, W., Obando, J., Lens, P.N.L., 2014. Spatial-temporal variability in water quality and macro-invertebrate assemblages in the Upper Mara River basin, Kenya. Phys. Chem. Earth 67-69, 93–104.

King, R.S., Baker, M.E., Whigham, D.F., Weller, D.E., Jordan, T.E., Kazyak, P.F., Hurd, M.K., 2005. Spatial Considerations for Linking Watershed Land Cover to Ecological Indicators in Streams. Ecol. Appl. 15, 137–153.

Kiptala, J.K., Mohamed, Y., Mul, M.L., Cheema, M.J.M., Van Der Zaag, P., 2013. Land use and land cover classification using phenological variability from MODIS vegetation in the Upper Pangani River Basin , Eastern Africa. Phys. Chem. Earth 66, 112–122.

Kizza, M., Rodhe, A., Xu, C., Ntale, H.K., Halldin, S., 2009. Temporal rainfall variability in the Lake Victoria Basin in East Africa during the twentieth century. Theor. Appl. Climatol. 98, 119–135.

Komakech, H.C., 2013. Emergence and Evolution of Endogenous Water Institutions in an African River Basin: Local Water Governance and State Intervention in the Pangani River Basin, Tanzania. IHE Delft University of Technology.

Komakech, H.C., Zaag, P. Van Der, 2011. Understanding the Emergence and Functioning of River Committees in a Catchment of the Pangani Basin , Tanzania. Water Altern. 4, 197–222.

Kuemmerlen, M., Reichert, P., Siber, R., Schuwirth, N., 2019. Ecological assessment of river networks : From reach to catchment scale. Sci. Total Environ. 650, 1613–1627.

Lalika, M.C.S., Meire, P., Ngaga, Y.M., 2015a. Exploring watershed conservation and water governance along Pangani River Basin, Tanzania. Land use policy 48, 351–361.

Lalika, M.C.S., Meire, P., Ngaga, Y.M., Chang'a, L., 2015b. Understanding watershed dynamics and impacts of climate change and variability in the Pangani River Basin , Tanzania. Ecohydrol. Hydrobiol. 15, 26–38.

Lammert, M., Allan, J.D., 1999. Assessing Biotic Integrity of Streams : Effects of Scale in Measuring the Influence of Land Use / Cover and Habitat Structure on Fish and Macroinvertebrates. Environ. Manage. 23, 257–270.

Ledger, M.E., Milner, A.M., 2015. Extreme events in running waters. Freshw. Biol. 60, 2455–2460.

Lewis, W.M., 2008. Physical and Chemical Features of Tropical Flowing Waters.In: D. Dudgeon, editor. Tropical Stream Ecology. Elsevier Inc., USA.

Li, L., Zheng, B., Liu, L., 2010. Biomonitoring and Bioindicators Used for River Ecosystems : Definitions , Approaches and Trends. Procedia Environ. Sci. 2, 1510–1524.

Lopez-Lopez, E., Sedeno-Diaz, J.E., 2015. Biological Indicators of Water Quality : The Role of Fish and Macroinvertebrates as Indicators of Water Quality Biological Indicators of Water Quality : The Role of Fish and Macroinvertebrates as Indicators of Water Quality. Environ. Indic. 643–661.

Lysyk, T.J., 2010. Species Abundance and Seasonal Activity of Mosquitoes on Cattle Facilities in Southern Alberta , Canada. J. Med. Entomol. 47, 32–42.

Mabidi, A., Bird, M.S., Perissinotto, R., 2018. Increasing salinity drastically reduces hatching success of crustaceans from depression wetlands of the semi-arid Eastern Cape Karoo region , South Africa. Sci. Rep. 8, 1–9.

Malmqvist, B., Rundle, S.D., 2002. Threats to the Running Water Ecosystems of the World. Environ. Conserv. 29, 134–153.

Masese, F.O., Kitaka, N., Kipkemboi, J., Gettel, G.M., Irvine, K., McClain, M.E., 2014. Macroinvertebrate functional feeding groups in Kenyan highland streams : evidence for a diverse shredder guild. Freshw. Sci. 33, 435–450.

Masikini, R., Tunu, L., Chicharo, L., 2018. Evaluation of ecohydrological variables in relation to spatial and temporal variability of macroinvertebrate assemblages along the Zigi River – Tanzania. Ecohydrol. Hydrobiol. 18, 130–141.

Mathew, M.M., Majule, A.E., Marchant, R., Sinclair, F., 2016. Variability of Soil Micronutrients Concentration along the Slopes of Mount Kilimanjaro , Tanzania. Appl. Environ. Soil Sci. 1–7.

Mathooko, J.M., Mavuti, K.M., 1992. Composition and seasonality of benthic invertebrates, and drift in the Naro Moru River, Kenya. Hydrobiologia 232, 47–56.

Mbonile, M.J., 2006. Population, Migration, and Water Conflicts in the Pangani River Basin, Tanzania, Environmental Change and Security Program Report.

Mbonile, M.J., 2005. Migration and intensification of water conflicts in the Pangani Basin, Tanzania. Habitat Int. 29, 41–67.

Meador, M. rR, Goldstein, R.M., 2003. Assessing Water Quality at Large Geographic Scales : Relations Among Land Use , Water Physicochemistry , Riparian Condition , and Fish Community Structure. Environ. Manage. 31, 504–517.

Mendoza, M.D., Montoya, J. V, Perez, B.Y., 2018. Diel periodicity of aquatic macroinvertebrate drift in a coastal stream in northern Venezuela. Neotrop. Biodivers. 4, 45–53.

Mereta, S.T., Boets, P., Ambelu, A., Malu, A., Ephrem, Z., Sisay, A., Endale, H., Yitbarek, M., Jemal, A., Meester, L. De, Goethals, P.L.M., 2012. Analysis of environmental factors determining the abundance and diversity of macroinvertebrate taxa in natural wetlands of Southwest Ethiopia. Ecol. Inform. 7, 52–61.

Mereta, T.S., Boets, P., De Meester, L., Goethals, P.L.M., 2013. Development of a multimetric index based on benthic macroinvertebrates for the assessment of natural wetlands in Southwest Ethiopia. Ecol. Indic. 29, 510–521.

Mesa, L.M., 2010. Effect of spates and land use on macroinvertebrate community in Neotropical Andean streams. Hydrobiologia 641, 85–95.

Metcalfe, J.L., 1989. Biological Water Quality Assessment of Running Waters Based on Macroinvertebrate Communities : History and Present Status in Europe. Environ. Pollut. 60, 101–139.

Miller, S.W., Judson, S., 2014. Responses of macroinvertebrate drift, benthic assemblages, and trout foraging to hydropeaking. Can. J. Fish. Aquat. Sci. 71, 675–687.

Minshall, G.W., Brock, J.T., Lapoint, T.W., 1982. Characterization and dynamics of benthic organic matter and invertebrate functional feeding group relationships in the Upper Salmon River, Idaho (USA). Int Rev Gesamten Hydrobiol 67, 793–820.

Minshall, G.W., Kenneth, C.W., Petersen, R.C., Cushing, C.E., Bruns, D.A., Sedell, J.R., Vannote, R.L., 1985. Developments in Stream Ecosystem. Can. J. Fish. Aquat. Sci. 42, 1045–1055.

Minshall, W.G., Petersen, R.C., Cummins, K.W., Bott, T.L., Sedell, J.R., Cushing, C.E., Vannote, R.L., 1983. Interbiome Comparison of Stream Ecosystem Dynamics. Ecol. Monogr. 53, 1–25.

Mitsch, W.J., Gosselink, J.G., 2000. Wetlands, 3rd ed. John Wiley, New York.

Morley, S.A., Karr, J.R., 2002. Assessing and Restoring the Health of Urban Streams in the Puget Sound Basin. Conserv. Biol. 16, 1498–1509.

Mwamila, T.B., Kimwaga, R.J., Mtalo, F.W., 2008. Eco-hydrology of the Pangani River downstream of Nyumba ya Mungu reservoir , Tanzania. Phys. Chem. Earth 33, 695–700.

Naman, S.M., Rosenfeld, J.S., Richardson, J.S., 2016. Causes and consequences of invertebrate drift in running waters : from individuals to populations and trophic fluxes. Can. J. Fish. Aquat. Sci. 73, 1292–1305.

National Bureau of Statistics, 2013. The United Republic of Tanzania, 2012 Population and Housing Census, Population Distribution by Administrative Areas. Tanzania.

National Sample Census of Agriculture(NSCA), 2007. United Republic of Tanzania, Regional Report: Arusha Region: Volume Vb.

Ndaruga, A.M., Ndiritu, G.G., Gichuki, N.N., Wamicha, W.N., 2004. Impact of water quality on macroinvertebrate assemblages along a tropical stream in Kenya. Afr. J. Ecol. 42, 208–216.

Nhiwatiwa, T., Brendonck, L., Waterkeyn, A., Vanschoenwinkel, B., 2011. The importance of landscape and habitat properties in explaining instantaneous and long-term distributions of large branchiopods in subtropical temporary pans. Freshw. Biol. 56, 1992–2008.

Nhiwatiwa, T., Dalu, T., 2016. Seasonal variation in pans in relation to limno-chemistry , size , hydroperiod , and river connectivity in a semi-arid subtropical region. Phys. Chem. Earth 97, 37–45.

Nhiwatiwa, T., Dalu, T., Sithole, T., 2017. Assessment of river quality in a subtropical Austral river system : a combined approach using benthic diatoms and macroinvertebrates. Appl. Water Sci. 7, 4785–4792.

Nhiwatiwa, T., De Bie, T., Vervaeke, B., Barson, M., Stevens, M., Vanhove, M.P.M., Brendonck, L., 2009. Invertebrate communities in dry-season pools of a large subtropical river : patterns and processes. Hydrobiologia 630, 169–186.

Nicolet, P., Biggs, J., Fox, G., Hodson, M.J., Reynolds, C., Whitfield, M., Williams, P., 2004. The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. Biol. Conserv. 120, 261–278.

Oertli, B., Auderset, J., Castella, E., Juge, R., Lehmann, A., Lachavanne, J.-B., 2005. PLOCH : a standardized method for sampling and assessing the biodiversity in ponds. Aquat. Conserv. Mar. Freshw. Ecosyetems 15, 665–679.

Ollis, D.J., Dallas, H.F., Esler, K.J., Boucher, C., 2006. Bioassessment of the ecological integrity of river ecosystems using aquatic macroinvertebrates : an overview with a focus on South Africa. African J. Aquat. Sci. 2, 205–227.

Paillex, A., Castella, E., Carron, G., 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. J. North Am. Benthol. Soc. 26, 779–796.

Palmer, R.W., Taylor, E.D., 2004. The Namibian Scoring System (NASS) version 2 rapid bio-assessment method for rivers. African J. Aquat. Sci. 29, 229–234.

Payne, A.I., 1986. The ecology of tropical lakes and rivers. John Wiley & Sons, New York, USA.

PBWO/IUCN, 2007a. IUCN Water and Nature Initiative and Pangani Basin Water Board. River Health Assessment Final Report, Pangani River Basin Flow Assessment. Moshi, Tanzania.

PBWO/IUCN, 2007b. Pangani River System: State of the Basin Report 2007.Moshi, Tanzania.

Pearson, R.G., Boyero, L., 2009. Gradients in regional diversity of freshwater taxa. J. North Am. Benthol. Soc. 28, 504–514.

Perkins, D.M., Reiss, J., Yvon-Durocher, G., Woodward, G., 2010. Global change and food webs in running waters. Hydrobiologia 657, 181–198.

Peterson, E.E., Ver Hoef, J.M., 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks. Ecology 91, 644–651.

Peterson, E.E., Ver Hoef, J.M., Isaak, D.J., Falke, J.A., Fortin, M.-J., Jordan, C.E., McNyset, K., Monestiez, P., Ruesch, A.S., Sengupta, A., Som, N., Steel, A., Theobald, D.M., Torgersen, C.E., Wenger, S.J., 2013. Modelling dendritic ecological networks in space : an integrated network perspective. Ecol. Lett. 16, 707–719.

Poff, L.N., Olden, J.D., Pepin, D.M., Bledsoe, B.P., 2006. Placing Global Stream Flow Variability in Geographic and Geomorphic Contexts. River Res. Appl. 22, 149–166.

Pyke, C.R., 2005. Assessing Climate Change Impacts on Vernal Pool Ecosystems and Endemic Branchiopods. Ecosystems 8, 95–105.

Ramsar Convention Secretariat, 2016. An Introduction to the Convention on Wetlands (previously The Ramsar Convention Manual). Ramsar Convention Secretariat, Gland, Switzerland.

Resh, V.H., Norris, R.H., Barbour, M.T., 1995. Design and implementation of rapid assessment approaches for water resource monitoring using benthic macroinvertebrates. Aust. J. Ecol. 20, 108–121.

Rhazi, L., Grillas, P., Saber, E.-R., Rhazi, M., Brendonck, L., Waterkeyn, A., 2012. Vegetation of Mediterranean temporary pools : a fading jewel? Hydrobiologia 689, 23–36.

Rhazi, L., Grillas, P., Toure, M.A., Ham, L.T., 2001. Impact of land use in catchment and human activities on water, sediment and vegetation of Mediterranean temporary pools. C.R. Acad. Sci. Paris 324, 165–177.

Richards, C., Haro, R.J., Johnson, L.B., Host, G.E., 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. Biol. 37, 219–230.

Richardson, C.J., 1994. Ecological Functions and Human Values in Wetlands: A Framework for Assessing Forestry Impacts. Wetlands 14, 1–9.

Rosenberg, D.M.., Resh, V.H., 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. Ecology 75, 267–268.

Rostami, S., He, J., Hassan, Q.K., 2018. Riverine Water Quality Response to Precipitation and Its Change. Environments 5, 1–17.

Roth, N.E., Allan, J.D., Erickson, D.L., 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landsc. Ecol. 11, 141–156.

Sagar, P.M., Glova, G.J., 1992. Diel changes in the abundance and size composition of invertebrate drift in five rivers in South Island , New Zealand. New Zeal. J. Mar. Freshw. Res. 26, 103–114.

Sanchez-Fernandez, D., Abellan, P., Mellado, A., Velasco, J., Millan, A., 2006. Are water beetles good indicators of biodiversity in Mediterranean aquatic ecosystems ? The case of the Segura river basin (SE Spain). Biodivers. Conserv. 15, 4507–4520.

Schiff, R., Benoit, G., 2007. Effects Of Impervious Cover At Multiple Spatial Scales On Coastal Watershed Streams. J. Am. Water Resour. Assoc. 43, 712–730.

Schneider, D.W., Frost, T.M., Schneider, D.W., Frost, T.M., 2012. Habitat Duration and Community Structure in Temporary Ponds Habitat duration and community structure in temporary ponds. J. North Am. Benthol. Soc. 15, 64–86.

Seymour, M., Fronhofer, E.A., Altermatt, F., 2015. Dendritic network structure and dispersal affect temporal dynamics of diversity and species persistence. Oecologia 908–916.

Shaghude, Y.W., 2006. Review of Water Resource Exploitation and Landuse Pressure in the Pangani River Basin. West. Indian Ocean 5, 195–207.

Shaghude, Y.W., 2006. Review of Water Resource Exploitation and Landuse Pressure in the Pangani River Basin. West. Indian Ocean J. Mar. Sci. 5, 195–207.

Shi, P., Zhang, Y., Li, Z., Li, P., Xu, G., 2016. Influence of land use and land cover patterns on seasonal water quality at multi saptial scales. Catena 151, 182–190.

Shimba, M.J., Jonah, F.E., 2016. Macroinvertebrates as bioindicators of water quality in the Mkondoa River , Tanzania , in an agricultural area. African J. Aquat. Sci. 41, 453–461.

Siddig, A.A.H., Ellison, A.M., Ochs, A., Villar-leeman, C., Lau, M.K., 2016. How do ecologists select and use indicator species to monitor ecological change ? Insights from 14 years of publication in Ecological Indicators. Ecol. Indic. 60, 223–230.

Silver, C.A., Vamosi, S.M., 2012. Macroinvertebrate Community Composition of Temporary Prairie Wetlands : A Preliminary Test of the Effect of Rotational Grazing. Wetlands 32, 185–197.

Sinha, A., Chatterjee, N., Ormerod, S.J., Adhikari, B.S., Krishnamurthy, R., 2019. River birds as potential indicators of local- and catchment-scale influences on Himalayan river ecosystems River birds as potential indicators of local- and catchment-scale influences on Himalayan river ecosystems. Ecosyst. People 15, 90–101.

Sliva, L., Williams, D.D., 2001. Buffer Zone Versus Whole Catchment Approaches To Studying Land Use Impact On River Water Quality. Watater Res. 35, 3462–3472.

Spencer, M., Blaustein, L., 2001. Hatching Responses of Temporary Pool Invertebrates to Signals of Environmental Quality. Isr. J. Zool. 47, 397–417.

Spencer, M., Blaustein, L., Schwartz, S.S., Cohen, J.E., 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools : relationships with habitat size and permanence. Ecol. Lett. 2, 157–166.

Stanfield, L.W., Kilgour, B.W., 2012. How Proximity Of Land Use Affects Stream Fish And Habitat. River Res. Appl. 1–15.

Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation : Recent progress and future challenges. J. North Am. Benthol. Soc. 29, 344–358.

Syvitski, J.P.M., Cohen, S., Kettner, A.J., Brakenridge, G.R., 2014. Geomorphology How important and different are tropical rivers ? - An overview. Geomorphology 227, 5–17.

Tanzania National Sample Census of Agriculture, 2007. United Republic of Tanzania National Sample Census of Agriculture: Volume Vc: Region Report: Kilimanjaro Region.National Bureau of Statistics, Ministry of agriculture and Food Security, Ministry of Water and Livestock Development, Ministry of Cooperatives.

The Water Utilization (Control and Regulation)(Amendment) Act, 1981.

Thorp, J.H., Delong, M.D., 1994. The Riverine Productivity Model: An Heuristic View of Carbon Sources and Organic Processing in Large River Ecosystems. Oikos 70, 305–308.

Tockner, K., Schiemer, F., Baumgartner, C., Kum, G., Weigand, E., Zweimuller, I., Ward, J. V, 1999. The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. Regul. riversResearch Manag. 15, 245–258.

Tran, C.P., Bode, R.W., Smith, A.J., Kleppel, G.S., 2010. Land-use proximity as a basis for assessing stream water quality in New York State (USA). Ecol. Indic. 10, 727–733.

Tudesque, L., Tisseuil, C., Lek, S., 2014. Scale-dependent effects of land cover on water physico-chemistry and diatom-based metrics in a major river system , the Adour-Garonne basin (South Western France). Sci. Total Environ. 466-467, 47–55.

Tumusiime, J., Tolo, C.U., Dusabe, M., 2019. Reliability of the Tanzania river scoring system (TARISS) macroinvertebrate index of water quality : a case study of the river Mpanga system , Uganda. J. Freshw. Ecol. 34, 541–557.

Tumwesigye, C., Yusuf, S.K., Makanga, B., 2000. Structure and composition of benthic macroinvertebrates of a tropical forest stream , River Nyamweru , western Uganda. Afr. J. Ecol. 38, 72–77.

Turpie, J., Ngaga, Y., Karanja, F., 2005. Catchment Ecosystems and Downstream Water :The Value of Water Resources in the Pangani Basin, Tanzania , Lao PDR. IUCN Water, Nature and Economics Technical Paper No. 7, IUCN —The World Conservation Union, Ecosystems and Livelihoods Group Asia.

Tuytens, K., Vanschoenwinkel, B., Waterkeyn, A., Brendonck, L.U.C., 2014. Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. Freshw. Biol. 59, 955–968.

UNDP, 2014. Reducing Land Degradation on the Highlands of Kilimanjaro Region.

Van den Broeck, M., Waterkeyn, A., Rhazi, L., Grillas, P., Brendonck, L., 2015. Assessing the ecological integrity of endorheic wetlands , with focus on Mediterranean temporary ponds. Ecol. Indic. 54, 1–11.

Vannote, R.L., Minshall, G.W., Cummins, K., Sedell, J.R., 1980. The River Continuum Concept. Can J Fish Aquat Sci 37, 130–7.

Vannote, R.L., Minshall, W.G., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37, 130–137.

Vanschoenwinkel, B., Brendonck, L., Pinceel, T., Dupriez, P., Waterkeyn, A., 2013. Rediscovery of Branchipus schaefferi (Branchiopoda : Anostraca) in Belgium - notes on habitat requirements and conservation management. Belgian J. Zool. 143, 3–14.

Ver Hoef, J.M., Peterson, E.E., 2010. A Moving Average Approach for Spatial Statistical Models of Stream Networks. J. Am. Stat. Assoc. 105, 1–18.

Vondracek, B., Blann, K., Cox, C.B., Nerbonne, J.F., Mumford, K.G., Nerbonne, B.A., Sovell, L.A., Zimmerman, J.K.H., 2005. Land Use , Spatial Scale , and Stream Systems : Lessons from an Agricultural Region. Environ. Manag. Vol 36, 775–791.

Vörösmarty, C.J., Mcintyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Vo, C.J., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561.

Wang, G., Yinglan, A., Xu, Z., Zhang, S., 2014. The Influence of Land Use Patterns on Water Quality at Multiple Spatial Scales in a River System. Hydrol. Process. 28, 5259–5272.

Wang, M., Qi, S., Zhang, X., 2012. Wetland loss and degradation in the Yellow River Delta, Shandong Province of China. Environ. Earth Sci. 67, 185–188.

Wantzen, K.M., Ramirez, A., Winemiller, K.O., 2006. New vistas in Neotropical stream ecology-Preface. J. North Am. Benthol. Soc. 25, 61–65.

Wantzen, K.M., Yule, C.M., Mathooko, J.M., Pringle, C.M., 2008. Organic Matter Processing in Tropical Streams, in: Tropical Stream Ecology. pp. 43–64.

Ward, J. V, Stanford, J.A., 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regul. riversResearch Manag. 11, 105–119.

Ward, J. V, Tockner, K., 2001. Biodiversity : towards a unifying theme for river ecology *. Freshw. Biol. 46, 807–819.

Waterkeyn, A., Grillas, P., Anton-pardo, M., Vanschoenwinkel, B., Brendonck, L., 2011a. Can large branchiopods shape microcrustacean communities in Mediterranean temporary wetlands ? Mar. Freshw. Res. 62, 46–53.

Waterkeyn, A., Grillas, P., Brendonck, L., 2016. Experimental test of the ecosystem impacts of the keystone predator Triops cancriformis (Branchiopoda: Notostraca) in temporary ponds. Freshw. Biol. 61, 1392–1404.

Waterkeyn, A., Grillas, P., De Roeck, E.R.M., Boven, L., Brendonck, L., 2009. Assemblage structure and dynamics of large branchiopods in Mediterranean temporary wetlands : patterns and processes. Freshw. Biol. 54, 1256–1270.

Waterkeyn, A., Grillas, P., Vanschoenwinkel, B., Brendonck, L., 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. Freshw. Biol. 53, 1808–1822.

Waterkeyn, A., Vanoverbeke, J., Van Pottelbergh, N., Brendonck, L., 2011b. While they were sleeping : dormant egg predation by Triops. J. Plankton Res. 33, 1617–1621.

Waterkeyn, A., Vanschoenwinkel, B., Grillas, P., Brendonck, L., 2010. Effect of salinity on seasonal community patterns of Mediterranean temporary wetland crustaceans : A mesocosm study. Limnol. Oceanogr. 55, 1712–1722.

Weigel, B.M., Wang, L., Rasmussen, P.W., Butcher, J.T., Stewart, P.M., Simon, T.P., Wiley, M.J., 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the Northern Lakes. Freshw. Biol. 48, 1440–1461.

Weilhoefer, C., Pan, Y., 2008. The effects of river floodwaters on floodplain wetland water quality and diatom assemblages. Wetlands 28, 473–486.

Williams, D.D., 2006. The biology of temporary waters. Oxford Biology, pp. 268.

Williams, D.D., 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. J. North Am. Benthol. Soc. 15, 634–650.

Williams, P., Biggs, J., Fox, G., Nicolet, P., Whitfield, M., 2001. History,origins and importance of temporary ponds. Freshw. Biol. Assoc. 17, 7–15.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, D., 2003. Comparative biodiversity of rivers , streams , ditches and ponds in an agricultural landscape in Southern England. Biological 115, 329–341.

Wright, J.., Moss, D., Armitage, P.., Furse, M.., 1984. A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. Freshw. Biol. 14, 221–256.

Yule, C.M., Pearson, R.G., 1996. Aseasonality of benthic invertebrates in a tropical stream on Bougainville Island, Papua New Guinea. Arch. fur Hydrobiol. 137, 95–117.

Chapter 1

Seasonal variation in benthic macroinvertebrate assemblages and water quality in an Afrotropical river catchment, northeastern Tanzania

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Abstract

Population growth and economic development have resulted in increased water demands, threatening freshwater resources. In riverine ecosystems, continuous monitoring of the river quality is needed to follow up on their ecological condition in the light of water pollution and habitat degradation. However, in many parts of the world, such monitoring is lacking, and ecological indicators have not been defined. In this study, we assessed seasonal variation in benthic macroinvertebrate assemblages in a tropical river catchment in northeastern Tanzania, which is currently experiencing an increase in agricultural activities. We examined the potential of in-stream environmental variables and land-use patterns to predict the river macroinvertebrate assemblages, and also identified indicator taxa linked to specific water quality conditions. Macroinvertebrate abundance, taxon richness and TARISS (Tanzania River Scoring System) score were higher in the dry season most likely due to higher surface runoff from agricultural land and poorer water quality in the wet season. In the wet season macro invertebrates seem to be limited by chlorophyll-a, oxygen and phosphorous while in the dry season, when water flow is lower, nitrogen and turbidity become important. Substrate composition was important in both seasons. Given the fact that different selective filters limit macroinvertebrate assemblages in both seasons, a complete picture of water quality can only be established by monitoring in both seasons. Riparian buffer zones may help to alleviate some of the observed negative effects of agricultural activities on the river system in the wet season while limiting irrigation return flows may increase water quality in the dry season.

Keywords: biomonitoring; environmental conditions; land-use; indicator taxa; benthic macroinvertebrates; agricultural intensification, Ruvu River

1. Introduction

Human activities negatively affect the functioning of freshwater ecosystems globally, resulting in the deterioration of water quality, loss of biodiversity and loss of ecosystem services (Malmqvist and Rundle, 2002; Søndergaard and Jeppesen, 2007; Chakona et al., 2008; Dudgeon, 2010; Vorosmarty et al., 2010). Excessive nutrient inputs, flow alteration, loss of riparian buffer zone and sedimentation are among the major anthropogenic impacts on freshwater ecosystems (Hrodey et al., 2009; Nyenje et al., 2010; Dodds et al., 2013). Globally, it is estimated that about 65% of freshwater habitats are considered moderately to severely threatened (Dudgeon et al., 2005; Schowe and Harding, 2014). This is especially true for (sub) tropical developing countries where intensification of land-use for agriculture and poor disposal of untreated waste have markedly degraded rivers and streams (Dudgeon, 1992; Beyene et al., 2009; Dlamini et al., 2010; Nyenje et al., 2010; Paisley et al., 2011; Bere and Nyamupingidza, 2014)

The quality of aquatic resources is usually assessed using physical, chemical and biological characteristics. However, impact assessment based on water chemistry alone is insufficient (Dalu et al., 2017a), since it does not integrate water quality temporally (Bellinger et al., 2006; Dalu and Froneman, 2016). Biological monitoring of freshwater ecosystems is acclaimed to be a quick and cost-effective method for assessing ecosystem conditions (Ollis et al., 2006; Dallas et al., 2010; Li et al., 2010). It allows long-term environmental effects to be detected, providing a broad measure of their synergistic impacts (Dalu and Froneman, 2016). Among the potential biotic component available for biomonitoring, benthic macroinvertebrates are the most commonly used in many regions (Dallas, 1995; Li et al., 2010; Aschalew and Moog, 2015; Siddig et al., 2016; Nhiwatiwa et al., 2017b). This is because they are ubiquitous and abundant even in small streams and form a dominant component of stream food webs (Rosenberg and Resh, 1993; Resh et al., 1995; Barbour et al., 1999; Hering et al., 2006). Benthic macroinvertebrates are regarded as good indicator organisms because they show taxon-specific differences in sensitivity to pollution, are taxonomically diverse, and have an aquatic life span long enough to provide a record of environmental quality (Metcalfe, 1989; Barbour et al., 1999; Nhiwatiwa et al., 2017a).

Rivers and streams often vary over time and exhibit seasonal variability in factors such as hydrology, water chemistry and habitat availability (Allan and Castillo, 2007; Dallas, 2004). Riverine organisms have specific habitat requirements and seasonal variation in these conditions will therefore affect the structure of benthic macroinvertebrate assemblage (Dallas, 2004; Zhang et al., 2012). As a result, to use macroinvertebrates as indicators and interpret the functionality of these communities in the light of ongoing environmental change, it is necessary to take this seasonal variation into account. (Dallas, 2004; Kilonzo et al., 2014). A major challenge is to separate potential effects of natural in-stream factors (e.g., flow rate, substrate) on biota and water quality from those linked to pollution and anthropogenic disturbance (e.g., agricultural activities) (Kilonzo et al., 2014; Jun et al., 2016).

Local in-stream factors such as water velocity, substrate type and water chemistry have been shown to primarily structure the assemblage of benthic macroinvertebrates by shaping local habitat characteristics (Richards et al., 1997; Statzner et al., 1988; Sandin and Johnson, 2004; Brooks et al., 2005; Allan and Castillo, 2007). Water velocity, for example, presents a direct physical force to the organisms and affects other in-stream factors such as food and sediment delivery, and oxygen content (Poff et al., 1997; Sandin and Johnson, 2004; Belmar et al., 2013; Pan et al., 2013). In addition, variation in substrate composition, in particular, is essential for the existence of many macroinvertebrate species because substrata provide shelter, food sources, and protection from predators (Ciutti et al., 2004; Li et al., 2012; Jun et al., 2016).

Moreover, landscape factors such as land-use patterns have a strong influence on river water and habitat quality, and subsequently on its biotic components. Agricultural activities, for example, can incite erosion and runoff of sediments, nutrients, and pesticides in river systems, consequently affecting macroinvertebrate assemblages (Kilonzo et al., 2014; Kalkhoff et al., 2016; Nhiwatiwa et al., 2017a). Riparian clearance and subsequent increased solar radiation can lead to higher water temperature and alter fundamental biogeochemical processes such as respiration and inputs of dissolved organic carbon (Paulo et al., 2019). Several studies have linked land-use patterns to responses of benthic macroinvertebrate communities (Karaouzas et al., 2007; Zhang et al., 2012; Theodoropoulos et al., 2015; Bere et al., 2016). However, information from tropical regions and Africa in particular are still scarce (Masikini et al., 2018).

Although numerous studies on seasonal variations in benthic macroinvertebrate assemblages in river systems have been conducted in temperate region (e.g., Perona et al., 1999; Sporka et al., 2006; McCord and Kuhl, 2013), there is an increasing interest in tropical systems across the globe (Dudgeon, 2008; Qadir et al., 2008; Kilonzo et al., 2014; Jun et al., 2016). There is important variation in flow predictability in tropical rivers (Pearson, 2014) and stream macroinvertebrate assemblages can vary strongly both within and among catchments (Boulton et al., 2008; Pearson et al., 2017). As a result, it is difficult to generalize the relative importance of landscape and local factors affecting river ecosystems (Sandin and Johnson, 2004) and there is a need for more studies from different areas of the world, particularly from the tropics.

In Tanzania like many (sub) tropical African countries, assessment of river quality is mainly based on the analysis of physico-chemical water quality parameters (e.g., Kihampa et al., 2013; Selemani et al., 2017). Biological assessment of river quality conditions using benthic macroinvertebrates has become established albeit relatively recently (Elias et al., 2014; Kaaya et al., 2015). Thus far, only a few studies on benthic macroinvertebrates have been published (Elias et al., 2014; Kaaya et al., 2015; Shimba and Jonah, 2016; Masikini et al., 2018). But these are limited in resolution and most river systems have not been investigated. As a result, the association between macroinvertebrate assemblages and environmental conditions in river systems in Tanzania is still not fully understood and we are currently not able to assess potential anthropogenic impacts on river quality. Consequently, there is a need for integrated high-resolution studies supported by appropriate statistical models that try to achieve this goal.

The Ruvu River catchment (RRC) is a socio-economically important catchment in the upper Pangani River basin: a biodiversity hotspot area in northeastern Tanzania (IUCN Eastern Africa Programme, 2003). The catchment is experiencing increases in agricultural activities accompanied by overexploitation of water for irrigation (Shaghude, 2006; PBWO/IUCN, 2007). Despite the increasing anthropogenic pressure, thus far no study has addressed how land-use could affect seasonal variation in the river quality (i.e., the physico-chemical and biological condition of the river system) in the catchment. At the moment, it is also not known which macroinvertebrate indicator taxa may be linked with specific water quality conditions.

In this study, we reconstruct seasonal variation in physico-chemical water quality and benthic macroinvertebrate assemblages in a tropical river catchment in Tanzania and build models to explain this variation. We used a combination of more quantitative indicator species analysis (IndVal) and multivariate analyses (variation partitioning of redundancy models) to study links between benthic macroinvertebrate assemblages and environmental factors over an entire catchment during two different seasons. We specifically aimed to (i) assess seasonal trends in physico-chemical water quality and macroinvertebrate assemblages and distributions, and (ii) identify key environmental factors (i.e., in-stream environmental variables and land-use factors) that can explain variation in macroinvertebrate community composition in the RRC. We also aimed (iii) to identify macroinvertebrate indicator taxa for the different water quality conditions in the RRC. We hypothesized that macroinvertebrate assemblages would vary seasonally due to differences in environmental conditions and rainfall surface run off patterns. We initially hypothesized that land-use effects on river quality may be more pronounced in the rainy season due to higher surface runoff. On the other hand, lower flow rates might result in higher impacts in the dry season when pollutants could be present at higher concentrations. Given these contrasting conditions we expected that different taxa might be useful as indicator species in the dry season compared to the wet season.

2. Materials and Methods

2.1. Study area

The Ruvu River catchment (not to be confused with Ruvu River in the Wami basin in the Morogoro region, Tanzania) is located in the upper Pangani River basin in the Kilimanjaro region, Tanzania, and is one of the permanent rivers recharging the Nyumba ya Mungu dam (Fig. 1). The catchment lies between 3.0^o and 4.2^o S and 36.3^o and 38.1^o E in the northeastern part of Tanzania and covers approximately 25% of the total basin area. The area is drained by four main rivers and their tributaries: Ghona River (RH), Dehu River (RD), Soko River (RS), and Ruvu River (RV). The water in the catchment originates from natural springs (along the eastern slopes of Mt. Kilimanjaro) and Lake Jipe (recharges the Ruvu River). The altitude of the Ruvu River catchment ranges from 4000 meters to 650 meters a.s.l. Mean annual rainfall ranges from 2000 mm along the slopes of Mt. Kilimanjaro to 500 mm in the low lands (PBWO/IUCN, 2007). The rainfall has a bimodal pattern where long rains (*Masika)* are experienced in the months of March to May and the short rains *(Vuli)* which are less reliable normally coming in November and December (Kiptala et al., 2013). The river system is subjected to various sources of pollution including diffuse pollution from agricultural activities (e.g., soil erosion, fertilizer run-off), sewage and domestic waste (*personal observations*).

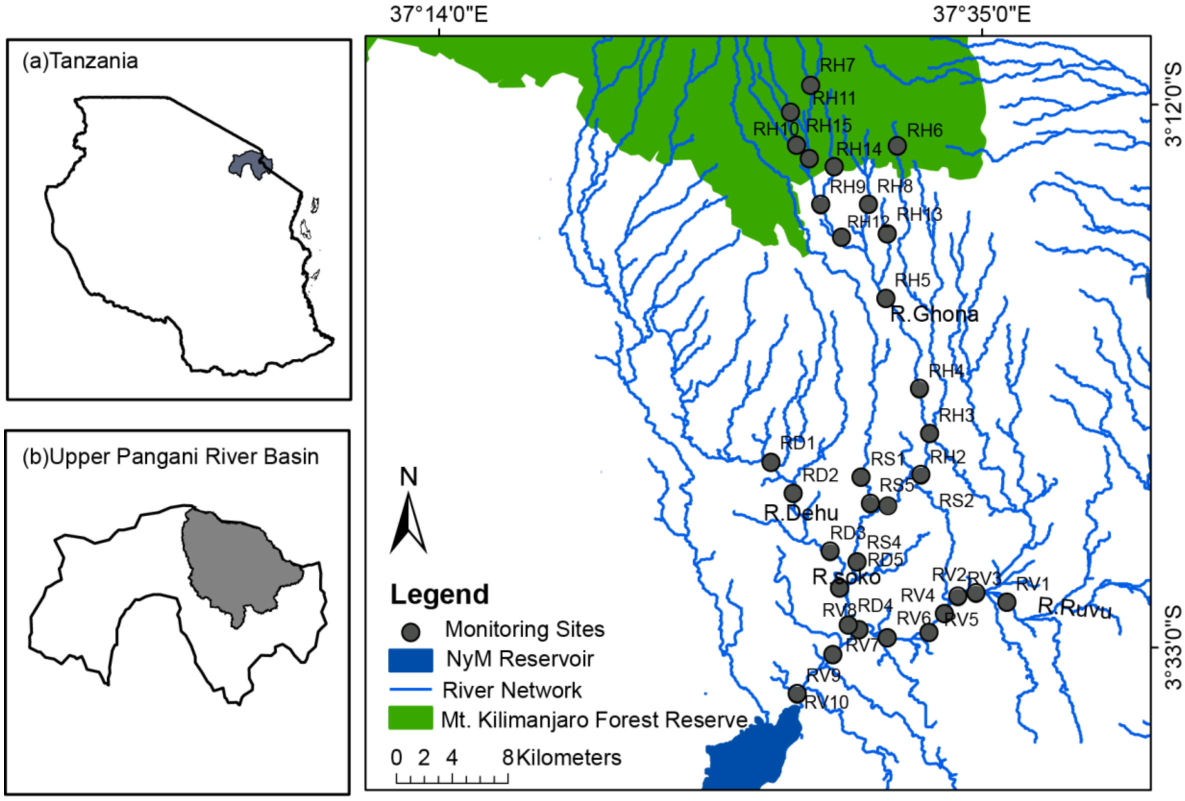


Fig.1. Map of the Ruvu River catchment showing the location of the of the twenty-nine monitoring sites. Inserts: (a) map of Tanzania with the location of the UPRB, and (b) map of UPRB with the location of the Ruvu River catchment. Abbreviations: RV=Ruvu River, RD=Dehu River, RH=Ghona River, RS=Soko River.

Economic activities follow the escarpment with Afrotropical montane rain forest (along the Mt. Kilimanjaro forest reserve) and multi-strata agroforestry (with intercropped coffee and banana plantations as main crops, and livestock keeping including dairy cattle, goats and pigs) in the upper reaches (Mathew et al., 2016). The middle and lower reaches consist of savanna bushland, small and large scale irrigated agriculture (common grown crops are rice, maize, beans, sisal, sugarcane, vegetables and fruits), herding, fishing and small industries (UNDP, 2014; Mathew et al., 2016). Mbonile (2005) and PBWO/IUCN (2007) reported higher population density in the upper Pangani River

Basin because of more favorable living conditions and the availability of fertile soils for agriculture, in particular. Approximately 80% of the population is engaged in agriculture and irrigation consumes most (up to 64%) of the available freshwater resources (Kiptala et al., 2013).

2.2. Study design

A total of 29 monitoring sites in the Ruvu River catchment (Fig.1 and Table S1 (Supplementary Information)) were sampled both in the dry (August–September 2015) and in the wet season (April–May 2016) to capture seasonal patterns in environmental variables and benthic macroinvertebrate assemblages. The sampled sites included four main rivers, namely Ghona River (RH), Dehu River (RD), Soko River (RS), and Ruvu River (RV) which drain to form the Ruvu River catchment (stream orders 1–3). The spatial gradient consisted of a ~ 51km longitudinal distribution of monitoring sites from upstream to downstream. Along this gradient, there was variation in land-use activities (Table S1).

2.3. Environmental variables sampling and analysis

Water samples were collected once in each season. At each sampling time, two water samples (n=2) were taken across the river section at each monitoring site. Water samples were collected using high density polyethylene (HDPE) 1-litre bottles. The bottles were washed and rinsed with distilled water and left overnight with 5 % hydrochloric acid solution (HCL). Prior to sampling, the bottles were rinsed again three times with sample water on site. Samples were collected by inserting the bottles at mid-depth in the river in the opposite direction of the river current (APHA, 2012). The samples were transported in an ice cooler box to the laboratory of the Department of Water Environmental Science and Engineering (WESE), at the Nelson Mandela African Institution of Science and Technology (NM-AIST) Arusha, Tanzania for analysis. In the laboratory, samples were preserved at 4 °C to stop the metabolism and all activities of the organisms in the water prior the analysis (APHA, 2012). The water analysis was done within 48 hours after sampling.

On each sampling occasion, electric conductivity (EC), temperature, pH, chlorophyll-a (Chl-a), turbidity (Turb), and dissolved oxygen (DO) were measured *in situ* at each monitoring site. Turbidity was determined using a HANNA-portable turbidity meter (Model-HI93703). Chlorophyll-a was measured using an AquaFluor Handheld Fluorometer (Model-8000-010). Fluoride (F^-) was determined using an ion selective electrode (Mettler Toledo SevenCompact™ pH/Ion S220). DO, pH, and EC, were measured using a HANNA multi-parameter instrument (Model-HI 9829). Chemical measurements of orthophosphate (PO_4^{3-}), nitrate (NO_3^--N), ammonium ($NH4^+$-N), total phosphorus (TP), total nitrogen (TN), and chemical oxygen demand (COD) were carried out in the laboratory using a portable spectrophotometer (Model HACH-DR 2800). Orthophosphate concentration was measured using an ascorbic acid (PhosVer 3) method (range: 0.02 to 2.50 mg/L PO_4^{3-}), nitrate concentration was measured using a cadmium reduction method (range: 0.01 to 30.0 mg/L NO_3^--N), ammonium was measured using the Nessler method (range: 0.02 to 2.50 mg/L $NH4^+$-N), total phosphorus was measured using PhosVer3 with acid persulfate digestion method (range: 0.06 to 3.50 mg/L PO_4^{3-}), total nitrogen was measured using a persulfate digestion method (range: 0.1 to 25.0 mg/L N), and chemical oxygen demand was measured using a reactor digestion method (range: 0.7 to 150.0 mg/L COD). All chemical analyses followed the standard methods for the examination of water and wastewater by APHA (2012).

Depth, flow velocity and substrate composition were measured at each monitoring site. For flow measurement, measuring tape was stretched between the endpoints of the river channel cross-section at each monitoring site. Then the cross-section distance was divided into cells/intervals (between 0.5m to 1m) depending on river width. At each cell the width, depth(m), and velocity(m/s) were measured. Flow velocity was measured using a Seba Universal Current Flow Meter F1 positioned at 0.60m water depth. Water depth was determined using a graduated measuring rod, held in a vertical position with the meter directly into the flow. The propeller or sensor was kept completely under water, facing into the current for 30 seconds and free of interference. The meter was adjusted slightly up or downstream to avoid snags, boulders, and other obstructions. Substrate composition was visually assessed following Minshall (1984), based on the following size class categories: (silt/mud < 0.06 mm), sand (0.06–2 mm), gravel (2–64mm), cobbles (64–256mm) and boulders (>256 mm). The dominant substrate type at each monitoring site was noted. A digital Elevation Model (DEM) (30 m resolution) was used to delineate the catchment boundaries using the hydrology tools using ArcGIS 10.2 desktop GIS software (ESRI Company, Redlands, California, USA).

Data on land-use categories in the catchment were obtained from Kiptala et al. (2013). In this study, land-use types were reclassified into seven major classes: (1) Water bodies; (2) Bare land; (3) Shrub land; (4) Agricultural land; (5) Afromontane forest; (6) Agroforestry; and (7) Wetland and swamps (Fig.2, Table S2; Supplementary information). Land-use information/data was derived as percentage (%) composition of each land-use type of a catchment area upstream of each monitoring site using ArcMap 10.2 (i.e., the perimeter of the quantified land-use types was the full catchment area upstream of each monitoring site).

2.4. Macroinvertebrate sampling, identification and counting

Macroinvertebrates were collected in a semi-quantitative way using a kick net of 1mm mesh size on a 30-cm square frame following the TARISS sampling protocol (Kaaya et al., 2015). Samples were collected from the dominant habitat type present at each site (i.e., the habitat that covers about 70% of the 50 m stretch making up the river section at the site). Sampled habitat types included (i) stones in-current (cobbles, boulders and bedrock), (ii) vegetation/macrophyte, and (iii) gravel/sand/mud (GSM). Stones and GSM habitats were sampled for one minute by kicking, turning or scraping them with the feet, whilst continuously sweeping the net through the disturbed area. The vegetation/macrophyte habitat was sampled by pushing the net vigorously and repeatedly against and through the vegetation over an area of approximately two meters. All drifting material collected in the kick net was stored in a labeled plastic container with 70% ethanol and transported to the laboratory for sorting and identification. In the laboratory, samples were washed with tap water using a 0.5mm mesh sieve then transferred into a white tray to sort out all macroinvertebrate specimens before preservation in 70% ethanol. The macroinvertebrates were identified with a dissecting microscope (10X magnification) to family level using different identification keys (Croft, 1986; Davies and Day, 1998; Gerber and Gabriel, 2002). It is well recognized that the relationship between macroinvertebrate assemblages and the environment is best performed using species-level identification (Fugère et al., 2016; Dalu et al., 2017b), however, family richness and species richness often correlate strongly in stream invertebrate communities, and the same key environmental factors seem to drive assemblage composition at the family species level (Fugère et al., 2016). Thus, family level identification has shown to be sufficient to detect effects of environmental disturbances such as pollution (Kaaya et al., 2015; Dalu et al., 2017b). It should also be noted that identification to species level is often difficult because of inadequate taxonomic knowledge.

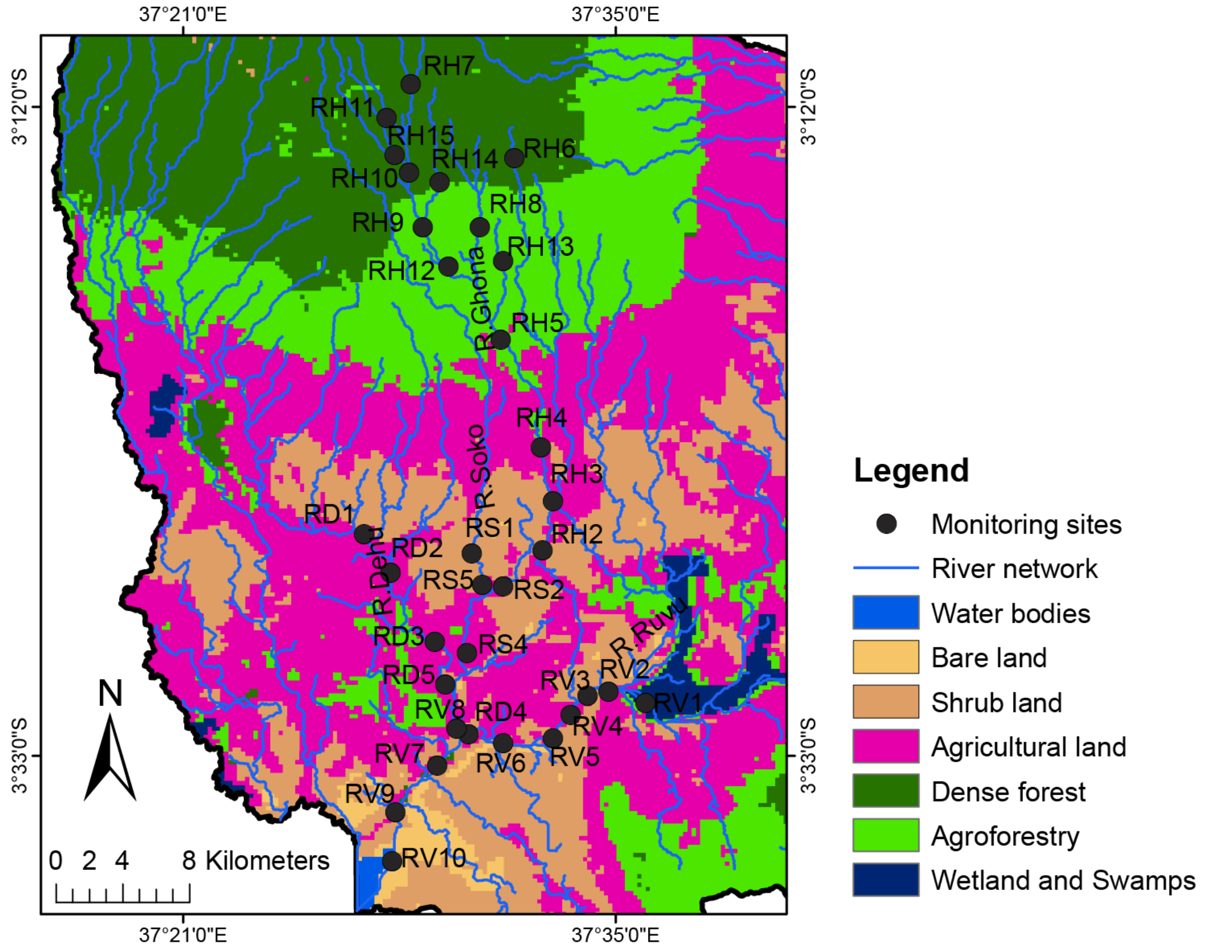


Fig.2. Map showing the spatial distribution of seven land-use classes in the Ruvu River catchment in relation to the river monitoring sites. (Source: Kiptala et al., 2013). Abbreviations: RV= Ruvu River, RD= Dehu River, RH=Ghona River, RS= Soko River.

2.5. Data Analysis

As macroinvertebrate biotic indices, we used taxon richness (number of Taxa (Taxa_S)) and the TARISS score. The latter index was developed specifically for river macroinvertebrates in Tanzania: designed for assessing ecological condition of river systems in the country. It takes high values when a site contains many sensitive taxa. The index was calculated following Kaaya (2014) by summing up taxon specific sensitivity weighting scores for each site. This index therefore does not consider the abundance. The sensitivity weighting ranges from 1 to 15, with values > 10 indicating taxa less tolerant to pollution.

Given that several variables could not generate acceptable normal distributions of residuals necessary for parametric tests (Shapiro Wilk test, $p \geq 0.05$), therefore, we opted for the non-parametric Wilcoxon signed rank test (Wilcoxon, 1945) at 95% confidence level to test for significant differences in macroinvertebrate biotic indices and environmental variables between seasons.

Generalized linear models with a Poisson error distribution were used to study the relationship between environmental variables (i.e., land-use and in-stream environmental variables) and macroinvertebrate biotic indices (i.e., taxon richness and TARISS score). The Poisson error distribution is appropriate for modelling community count data with many zeros (O'Hara and Kotze, 2010). A backward selection followed by a forward selection was computed to eliminate non-significant environmental variables from the models using the function *step* in the vegan package (Oksanen et al., 2016) in R (version 3.1.2, R Core Team, 2014). The procedure aimed to maximize the potential variation in macroinvertebrate biotic indices that can be explained by environmental variables. The Akaike information criterion (AIC) and Mc Fadden's pseudo R^2 coefficient (R^2_{pseudo}) were used to determine the model with the best subset of environmental predictor variables. The AIC is an estimator of the relative quality of statistical models for a given set of data; it estimates the quality of each model relative to each of the other models (Akaike, 1974). The chosen 'best' model is the one that minimizes the Kullback-Leibler distance between the model and the data, and has a minimum AIC (most parsimonious model) compared to all the other models (Burnham and Anderson, 2002). The latter (i.e. R^2_{pseudo}) is a simple measure for model fit for generalized linear models. R^2_{pseudo} coefficients are typically much smaller than conventional R^2 coefficients, values between 0.2 and 0.4 already indicate excellent model fit. Prior to this analysis, the explanatory variables were tested for correlation using Spearman rank correlations to prevent multicollinearity in the models. For example, total-P and orthophosphate were strongly correlated so we only included total-P in the model, while acknowledging in our interpretation that this gradient also reflects orthophosphate.

We tested for the effect of environmental variables (i.e., land-use and in-stream environmental variables) on macroinvertebrate community composition using separate redundancy analyses (RDA), a multivariate extension of multiple regression. Prior to analysis, macroinvertebrate count data were

Hellinger transformed to improve the performance of ordination with community composition data containing many zeros (Legendre and Gallagher, 2001; Zuur et al., 2007). Rare taxa that occurred in less than three sites were not included in the analysis as this is insufficient to model their distributions. The significance of the RDA models was assessed with Monte-Carlo permutations (nperm= 999). A forward selection procedure was performed to retain only significant variables in the models. The relationships between the most important explanatory variables (retained in the model by forward selection) and macroinvertebrate community composition (Hellinger transformed taxon abundance data) were visualized using a Principal Component Analyses (PCA) ordination plot. The environmental variables were added in the plot as supplementary variables that do not affect the ordination. Taxa for which less than 30 percentage of variation was captured by the plot were not shown.

In addition, the relative importance of local in-stream environmental variables and land-use variables in terms of explaining macroinvertebrate assemblages was quantified using a variation partitioning procedure. This procedure based on partial redundancy analyses (pRDA) (Legendre and Lengendre, 2012) allows to partition the total amount of variation in macroinvertebrate assemblages, and to be decomposed into fractions explained by different sets of explanatory variables (Legendre and Lengendre, 2012). It defines a fraction of unexplained variation, fractions that are uniquely explained by land-use or in-stream environmental variables, respectively, and a third fraction that captures the variation explained by the covariation between land-use and local in-stream environmental conditions.

Finally, the IndVal i.e., indicator species method was used to detect indicator taxa linked to different water quality classes (Dufrêne and Legendre, 1997; De Cáceres et al., 2010). The studied sites were categorized *a priori* in good, intermediate/fair and poor water quality categories using the TARISS score (Kaaya et al., 2015); good: TARISS >80, intermediate/fair: TARISS 50–80; poor: TARISS < 50. The classification was based on the Gower distance matrix and a hierarchical clustering analysis (Ward method) (Dufrêne and Legendre, 1997; Borcard et al., 2011). A good indicator taxon is mostly found in one site class and is present in most sites belonging to that class. The indicator value of a taxon varies between 0 and 1, attaining its maximum value when all individuals of one taxon occur in all sites of a single site class (Dufrêne and Legendre, 1997; Heino et al., 2005; Lumbreras et al., 2016). The significance of the indicator values for each taxon were tested via Monte-Carlo permutations (nperm=999). The indicator value has two components; (i) a specificity/predictive value (component A) and (ii) a sensitivity/fidelity (component B). Specificity (A) is the probability that the surveyed site belongs to the target site class given the fact that the taxon has been found, while sensitivity (B) is the probability of finding the taxon in sites belonging to the site class.

All analyses of macro invertebrate assemblages were performed separately for the dry and the wet seasons to be able to contrast different drivers of diversity and assemblage structure. All statistical tests were performed in R version 3.1.2 (R Core Team, 2014) using the packages vegan, permute, packfor and indicspecies.

3. Results

3.1. Environmental variables

The summary statistics of the measured water quality variables are presented in Table S3 (Supplementary Information) as mean ± standard deviation (SD). Significant differences between dry and wet seasons (Wilcoxon signed rank test, $p < 0.05$) were observed for chemical oxygen demand, total nitrogen, chlorophyll-a, turbidity and fluoride, Table1 and Fig.S1 (Supplementary Information). Concentrations of phosphate, ammonia and nitrate showed no significant seasonal variation (Wilcoxon signed rank test, $p > 0.05$), however, the concentrations were higher in the wet than in the dry season, Table 1. Wilcoxon signed rank tests also showed significant differences in average velocity and average water depth (Wilcoxon signed rank test, $p < 0.05$) between wet and dry seasons (Table 1).

3.2. General patterns of macroinvertebrate community structure

A total of 7530 macroinvertebrates corresponding to 54 families were collected in both the dry and the wet seasons (Table S4; Supplementary Information). The main taxonomic groups were Trichoptera, Ephemoroptera, Coleoptera, Hemiptera, Plecoptera, Odonata, Decapoda, and Gastropoda. Diptera were the most diverse taxon with nine families, followed by Hemiptera with eight families, Coleoptera with seven families, and Ephemeroptera, Trichoptera and Odonata with five families each. Macroinvertebrate abundances, taxon richness and TARISS score were all higher in the dry season than in the wet season (Wilcoxon signed rank test, $p < 0.05$ (Table 1, Fig. S2; Supplementary Information).

3.3. The effect of environmental variables on macroinvertebrate biotic indices

Environmental variables significantly explained variation in taxon richness (dry: AIC =175.68, $R^2_{\text{Pseudo}} = 0.27$; wet: AIC =111.71, $R^2_{\text{Pseudo}} = 0.21$) and TARISS scores (dry: AIC = 578.94, $R^2_{\text{Pseudo}} = 0.51$; wet: AIC =233.27, $R^2_{\text{Pseudo}} = 0.69$), Table 2. A backward followed by forward selection identified different sets of significant environmental variables for taxon richness and TARISS scores, but land-use (forest and cropland, agricultural land, dense forest, and shrub land and thickets) and substrate composition had a significant effect on all the biotic indices in both seasons, Table 2. In the dry season communities were limited by nitrogen, water velocity and turbidity while in the wet season chlorophyll-a, oxygen and phosphorous become important in explaining variation in taxon richness and TARISS scores.

Table 1 Results of Wilcoxon signed rank tests for environmental variables and macroinvertebrate biotic indices between dry and wet seasons in the Ruvu River catchment showing the z-statistics and p-values. Significance levels are indicated as follows: ***= p < 0.001, ** = p < 0.01, and * = p < 0.05.

Variables		**Mean Values**		**Wilcoxon rank sum test**	
		Dry season	**Wet season**	z	*p*
Environmental	pH	7.67	7.71	-0.144	0.895
	Electric Conductivity (µS/cm)	491.37	523.55	-0.137	0.899
	Dissolved oxygen (mg/L)	6.64	6.85	-0.216	0.838
	Temperature (°c)	23.81	20.26	-0.174	0.651
	Chlorophyll a (µg/L)	90.05	32.04	**-4.541**	**0.001*** **
	Turbidity (ftu)	9.23	40.79	**4.197**	**0.001*** **
	Fluoride (mg/L)	0.24	0.16	**-2.739**	**0.006** **
	Ammonium (mg/L)	0.15	0.18	-1.270	0.209
	Nitrate (mg/L)	0.59	0.91	0.483	0.638
	Orthophosphate (mg/L)	0.57	0.74	-0.631	0.418
	Total Phosphorus (mg/L)	0.81	1.37	0.985	0.331
	Total Nitrogen (mg/L)	0.89	1.53	**1.754**	**0.042* **
	Chemical Oxygen Demand (mg/L)	15.90	30.10	**2.823**	**0.005** **
	Average velocity (m/s)	0.38	1.29	**4.541**	**0.001*** **
	Average depth (m)	0.42	0.76	**4.469**	**0.001*** **
Macro-invertebrates	Abundance	237.48	41.41	**1.714**	**0.046* **
	TARISS Score	64.15	33.33	**-3.400**	**0.001*** **
	Taxon richness	10.0	4.74	**-3.747**	**0.001*** **

Table 2 Results of the generalized linear models with AIC and coefficients of determination R^2_{pseudo}, z-statistic and p-value of the most important explaining variables of the selected models for macroinvertebrate taxon richness and TARISS score in the Ruvu River catchment. Models are based on a backward followed by forward selection procedure aimed to maximize the potential variation in macroinvertebrate indices that can be explained by environmental variables. Significance levels are indicated as follows: ***= p < 0.001, ** = p < 0.01, and * = p < 0.05. A (+) sign refers to a positive association, (-) sign refers to a negative association, and (ns) refers to not significant.

Explaining Variables	**Seasons**							
	Dry				**Wet**			
	Richness		**TARISS**		**Richness**		**TARISS**	
	AIC =175.68 $R^2_{Pseudo} = 0.27$		AIC = 578.94 $R^2_{Pseudo} = 0.51$		AIC =111.71 $R^2_{Pseudo} = 0.21$		AIC =233.27 $R^2_{Pseudo} = 0.69$	
	z value	**p value**	**z value**	**p value**	**z value**	**p value**	**z value**	**p value**
Dissolved oxygen	ns	ns	ns	ns	ns	ns	2.625	0.008 **
Chlorophyll-a	ns	ns	6.281	0.0001***	1.858	0.036*	ns	ns
Turbidity	-4.385	0.0001***	-2.354	0.038*	ns	ns	ns	ns
Ammonia	-2.691	0.007 **	-4. 982	0.012*	ns	ns	ns	ns
Nitrate	ns	ns	ns	ns	-1.761	0.044*	ns	ns
Total nitrogen	2.445	0.014*	ns	ns	ns	ns	ns	ns
Total phosphorus	ns	ns	ns	ns	ns	ns	-2.628	0.008 **
Velocity	-2.574	0.01*	-2.830	0.005**	ns	ns	ns	ns
Substrate: GSM (gravel/sand/mud)	-4.466	0.0001***	-6.622	0.0001***	-1.511	0.028*	-3.655	0.0001***
Substrate: Stones (cobbles/boulders/ bedrock)	ns	ns	9.395	0.001***	ns	ns	2.669	0.007 **
% Agricultural land	-4.168	0.001**	-5.354	0.0001***	-3.386	0.002**	-3.441	0.003**
% Dense forest	ns	ns	1.967	0.034*	2.936	0.006**	ns	ns
% Forest and cropland	4.239	0.001**	2.132	0.004**	ns	ns	2.271	0.001**
% Shrub land	-1.697	0.032*	ns	ns	ns	ns	-1.914	0.018*

3.4. The influence of environmental variables on macroinvertebrate assemblages

Generally, there was a significant effect of environmental variables on the macroinvertebrate assemblages both in the dry (in-stream variables: F=3.38, p=0.001; land-use: F=3.165, p=0.002) and in the wet (in-stream variables: F=5.22, p=0.001; land-use: F=4.95, p=0.01) seasons, Table 3. Local in-stream factors explained 36% and 32% of the total variation in the composition of macroinvertebrates in the dry and wet seasons respectively. Land-use explained 23% and 21% of the total variation in the composition of macroinvertebrates in the dry and wet seasons respectively. Forward selection identified different sets of significant environmental variables for macroinvertebrates between seasons, but substrate type (in-stream environmental factor) and land-use (agricultural land and shrub land and thickets) had a significant effect on macroinvertebrate assemblage in both seasons, Table 3. The PCA ordination plot for the visualization of the relationship between macroinvertebrate community composition (Hellinger-transformed macroinvertebrates abundance data) and the most important explanatory variables retained in the forward selection plotted as supplementary variables (separately for the in-stream and land-use variables) for the dry and wet seasons are presented in Fig. 3.

Variation partitioning analyses revealed that the overall effect of in-stream environmental variables and land-use on macroinvertebrate community composition was similar in the dry season, Fig. 4. In the wet season, the direct effect of land-use on macroinvertebrate community composition was relatively higher than the in-stream environmental conditions, Fig. 4. A considerable fraction of compositional variation in macroinvertebrate community was explained by shared effects between in-stream environmental conditions and land-use factors.

Table 3 Results of the RDA analyses showing the global F, p-value and coefficients of determination (R^2_{Adjusted}) of the full models, and F-statistic and p-value of the selected important environmental variables explaining macroinvertebrate assemblages in the Ruvu River catchment. Models are based on a forward selection procedure aimed to maximize the potential variation in macroinvertebrate assemblages that can be explained by environmental variables. Significance levels are indicated as follows: *** = $p < 0.001$, ** = $p < 0.01$, and * = $p < 0.05$.

Season	**Explaining Variable**	**F**	**p value**	**Global F**	**p value (global F)**	**R^2_{Adjusted}**
Dry	Instream variables			3.38	0.001 **	0.36
	Substrate	4.99	0.002**			
	Turbidity	2.62	0.011*			
	Ammonium	2.64	0.015*			
	Velocity	2.32	0.021*			
	Land-use variables			3.165	0.002**	0.23
	% Agricultural land	7.56	0.002**			
	% Shrub land and thickets	2.56	0.021*			
	% Agroforestry	2.03	0.034*			
Wet	Instream variables			5.22	0.001 **	0.32
	Substrate	2.01	0.040*			
	Chlorophyll-a	11.97	0.001**			
	Land-use variables			4.95	0.01*	0.21
	% Agricultural land	6.32	0.001**			
	% Shrub land	2.53	0.018*			

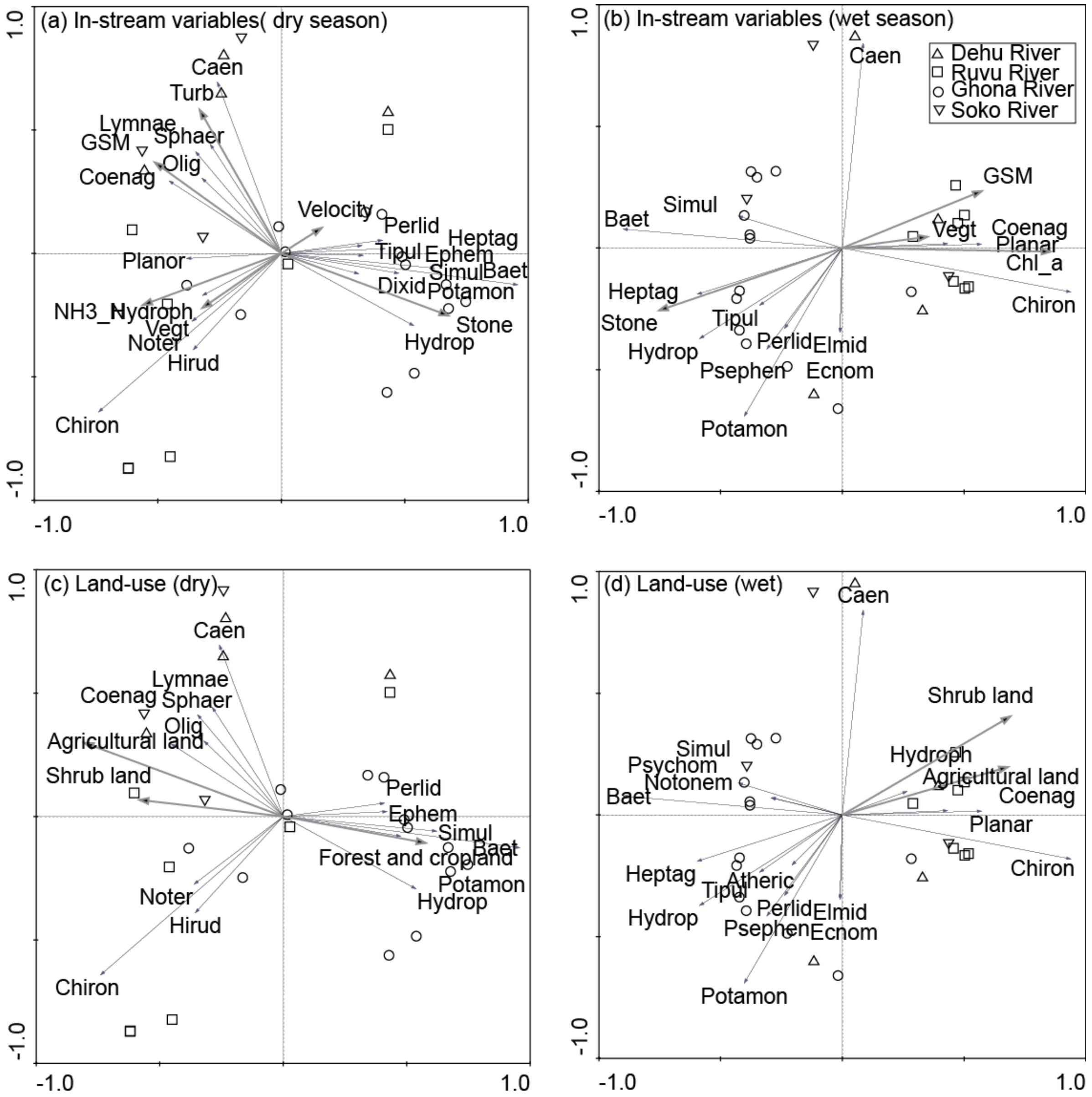


Fig.3. Principal component analysis ordination bi-plots illustrating the relationship between macroinvertebrate assemblages and the most important explanatory variables plotted as supplementary variables: (a and b) in-stream environmental variables, and (c and d) land-use variables in the dry and wet seasons. Only taxa with more than 30% contribution to the total variation are plotted. Baet=Baetidae, Caen= Caenidae, Heptag= Heptageniidae, Ephem= Ephemerythidae, Leptop= Leptophlebidae, Hydrop= Hydropsychidae, Ecnom= Ecnomidae, Leptoc= Leptoceridae, Philop= Philopotamidae, Hydrop= Hydroptilidae, Aesh= Aeshinidae, Libell= Libellulidae, Coenag= Coenagrionidae, Chlorocy= Chlorocyphidae, Olig= Oligochaeta, Hirud= Hirudinea, Physid= Physidae, Lymnae= Lymnaenidae, Planor= Planorbidae, Thiar= Thiaridae, Sphaer= Sphaeriidae, Hydrach=Hydrachnidiae, Gyrin = Gyrinidae, Elmid= Elmidae, Psephen= Psephenidae, Helod= Helodidae, Hydroph= Hydrophilidae, Torridin= Torridincolidae, Noter= Noteridae, Potamon= Potamonautidae, Atyid= Atyidae, Atheric= Athericidae, Taban= Tabanidae, Culic= Culicidae, Chiron= Chironomidae, Tipul= Tipulidae, Simul=

Simuliidae, Scyomyz= Scyomyzidae, Dixid= Dixidae, Psychod= Psychodidae, Ceratop= Ceratopogonidae, Empid= Empididae, Gerrid= Gerridae, Veliid= Veliidae, Naucor= Naucoridae, Pleid= Pleidae, Nepid= Nepidae, Hebrid= Hebridae, Corixid= Corixidae, Pyralid= Pyralidae, Perlid= Perlidae, Notonem= Notonemouridae, Planar= Planaridae, Turb=Turbidity, GSM=Gravel/Sand/Mud, RV= Ruvu River, RD= Dehu River, RH=Ghona River, RS= Soko River.

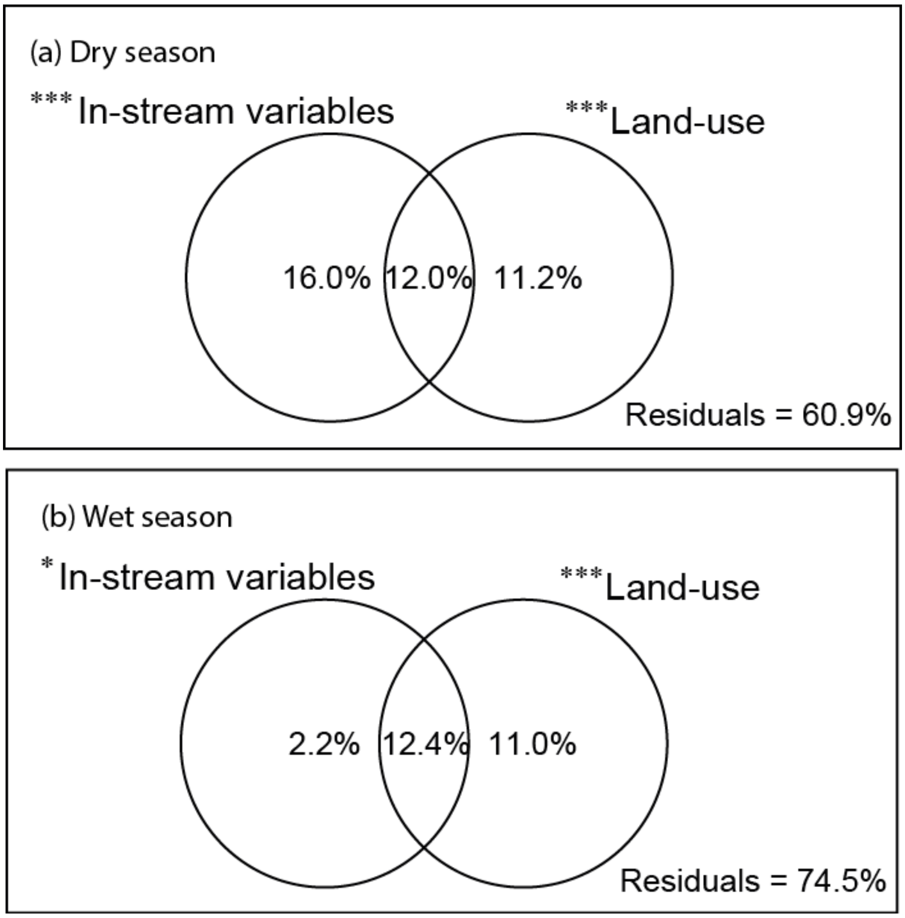


Fig.4. Unique and shared contributions of in-stream environmental variables and land-use variables on the macroinvertebrate assemblages in the (a) dry and (b) wet seasons. Significance levels are indicated as follows: *** = $p < 0.001$, ** = $p < 0.01$, and * = $p < 0.05$. Percentages represent explained variation by each component.

3.5. Indicator taxa

Hierarchical clustering diagrams for site classification are presented in Fig. S3. In the dry season, three families (Baetidae, Potamonautidae and Heptageniidae) were indicators of good water quality (see Table 4). Baetidae had the highest indicator value (IndVal=0.929), occurring in all good quality sites (B=1.000) and was largely restricted to it (A = 0.8628). Potamonautidae and Heptageniidae occurred only in good water quality sites (A=1.000). Thiaridae was an indicator taxon for intermediate water quality while Hirudinea and Hydrophilidae were indicators for poor water quality. Thiaridae occurred in all sites belonging to the intermediate water quality class (B=1.000) and was largely (but not completely) restricted to it (A=0.9541). Hirudinea and Hydrophilidae occurred in poor water quality sites only (A=1.000), though not all poor water quality sites were housing these families (B=0.444). In the wet season, three families (Baetidae, Hydropsychidae and Heptageniidae) were indicators of good water quality. Baetidae occurred in all good water quality sites (B=1.000) and they were almost completely restricted to these sites (A=0.9763). Hydropsychidae and Heptageniidae occurred only in sites with relatively good water quality (A= 1.000). Chironomidae were an indicator of poor water quality. Chironomidae occurred in all sites with relatively poor water quality (B=1.000) but were not completely restricted to these sites (A=0.6079).

Table 4 Results of the macroinvertebrate indicator taxon analysis listing indicator species for each water quality class (G= good, IM= intermediate and PR= poor) and for each season. Indicator values and associated P values are provided as well as the specificity (A) and sensitivity (B) scores. Significance levels are indicated as follows: *** = p < 0.001, ** = p < 0.01, and * = p < 0.05.

Season	Water Quality	Indicator taxa	Indicator Value	p value	A	B
Dry	**G**	Baetidae	0.929	0.008**	0.8628	1
		Potamonautidae	0.816	0.016*	1	0.6667
		Heptageniidae	0.73	0.043*	1	0.5333
	IM	Thiaridae	0.977	0.003**	0.9541	1
	PR	Hirudinea	0.667	0.044*	1	0.4444
		Hydrophilidae	0.667	0.045*	1	0.4444
Wet	**G**	Baetidae	0.988	0.001 **	0.9763	1
		Hydropsychidae	0.886	0.003 **	1	0.7857
		Heptageniidae	0.845	0.035 *	1	0.7143
	PR	Chironomidae	0.78	0.029*	0.6079	1
	IM + PR	Chironomidae	0.928	0.002**	0.9849	0.875

4. Discussion

In this study, we assessed seasonal variation in benthic macroinvertebrate assemblages and water quality in the Ruvu River catchment in northeastern Tanzania. Our findings indicate that physico-chemical water quality and macroinvertebrate community composition varied between seasons and that different sets of indicator taxa for water quality emerge in different seasons. Both in-stream environmental conditions and land-use factors influenced macroinvertebrates, but their relative importance also depended on the season. In the wet season macroinvertebrates seem to be limited by chlorophyll-a, oxygen and phosphorous while in the dry season, when water flow is lower, nitrogen and turbidity become important.

We initially hypothesized that land-use effects on river quality may be more pronounced in the rainy season due to higher surface runoff from agricultural land. This seems to be confirmed as macroinvertebrates were less abundant and showed lower diversity in the wet season. This may seem counter intuitive given that water volumes, and thus available habitat is larger in the wet season. However, most likely the higher nutrient concentrations (particularly phosphate) and turbidity levels eliminate some sensitive taxa during the wet season (e.g., Heptageniidae and Perlidae). This trend is confirmed in other studies of tropical rivers (Harding et al, 1999; Ndaruga et al., 2004; Bere et al., 2016; Nhiwatiwa et al., 2017a). Although diversity was higher and water quality was better, also in the dry season there was substantial variation in macroinvertebrate assemblages among sites, but these were driven by different variables. Lower water flow in this season due to lower precipitation and increased water abstraction via irrigation may lead to accumulation of nitrogen containing nutrients in some river sites and low oxygen conditions that can locally decrease water quality and exclude some taxa. Some taxa such as Hirudinea and Potamonautidae emerge as indicator species for poor and good water quality respectively in this season but not in the wet season. This is consistent with our second hypothesis and indicates that different selection pressures limit the occurrences and resulting diversity of macroinvertebrates in both seasons. Seasonal variation in discharge leads to differences in wetted perimeter, hydraulic conditions, and habitat availability which may also affect benthic macroinvertebrates (Dallas, 2004). Furthermore, the differences in macroinvertebrate community composition between seasons can also be partly due to the fact that different taxa show differential success between seasons according to their particular resilience or resistance traits (such as colonization and establishment abilities) (Blanchette and Pearson, 2013; Botwe et al., 2015).

The RDA and generalized linear models showed that water velocity, substrate type, turbidity and nutrients were the most important local in-stream environmental variables that explained macroinvertebrate community structure. Stream water velocity has been indicated in many studies to be strongly related to the community composition of benthic macroinvertebrates (e.g., Poff et al., 1997; Sandin and Johnson, 2004; Allan and Castillo, 2007; Belmar et al., 2013; Pan et al., 2013). This is because, the flow velocity configures stream morphology, bed stability, and consequently the availability of aquatic habitats for in-stream organisms (Belmar et al., 2013). For example, high flow velocity is regarded not only to scour macroinvertebrates directly but also determines other habitat conditions by influencing the transport of sediments (Poff et al., 1997; Sandin and Johnson, 2004; Belmar et al., 2013; Pan et al., 2013). As such, habitats are more stable during the dry season, thereby allowing longer time macroinvertebrates colonization and subsequently increment of the species number and abundance (Principe et al, 2007). In addition, water velocity also affects in-stream food delivery and oxygen content (Sandin and Johnson, 2004; Allan and Castillo, 2007) which directly affects the existence of in-stream biota.

Substrate type was important both in the dry and the wet season. Macroinvertebrate biotic indices were positively correlated with the stone substratum while negatively associated with GSM substratum. Stone substratum, particularly cobbles, has been indicated to support a large number of benthic macroinvertebrate taxa due to the availability of diverse microhabitats that provide refuge from currents and predation, attachment for filter-feeding taxa, food for herbivores and detritivores, and exit points for emerging insects with aerial adult stages (Brooks et al., 2005; Allan and Castillo, 2007; Pan et al., 2013; Jun et al., 2016). In contrast, habitats with fine substrate support few macroinvertebrate taxa: this is related to habitat instability, detritus shortage, and unavailability of refugia (Principe et al., 2007; Chakona et al., 2008). Similarly, several other studies conducted elsewhere have reported a strong correlation between substrate type and macroinvertebrate communities (Ciutti et al., 2004; Sandin and Johnson, 2004; Li et al., 2012; Jun et al., 2016). Li et al. (2012) indicated that substratum degradation can perturb the macroinvertebrate community even when water quality remains good. In our study area fine sediment from agricultural land can cover valuable gravel and cobble habitat for macroinvertebrates. Hence, part of the substrate effect we detected in this paper may still be traced to negative impacts of agriculture.

Our study showed that agricultural and shrub land and thickets land-use types were the most important land-use variables influencing macroinvertebrate assemblages in both seasons. The responses were reflected in the declines in taxon richness and TARISS scores with agricultural land-use. These relationships were consistent with other studies describing changes in macroinvertebrate communities in agricultural catchments (Richards et al., 1996; Allan, 2004; Collier, 2008; Magierowski et al., 2012; Nhiwatiwa et al., 2017a). These patterns may be driven by multiple mechanisms common to all agricultural land-use, such as changes in water quality, habitat alteration, loss of riparian zones and dominance of fine sediments (Magierowski et al., 2012; Botwe et al., 2015). The remaining unexplained variation in macroinvertebrate assemblages might be a result of other gradients such as pesticide and heavy metal concentrations, biotic interactions (Al-shami et al., 2011; Nhiwatiwa et al., 2017a), or a set of multiple stressors (Dalu et al., 2017b) which were not quantified in our study.

The variation partitioning showed that in-stream environmental variables and land-use explain similar amounts of variation in macroinvertebrate communities in the dry season. In contrast, the unique effect of land-use explained a substantial fraction of variation in macroinvertebrate assemblages in the wet season. This pattern could result from intensified agricultural activity during the wet season. Studies show that agricultural activities tend to have more negative impacts on invertebrate diversity and community structure when agriculture exceeds 40 percent of the watershed land-use (Genito et al., 2002; Boyer-Rechlin et al., 2016). This is true for the Ruvu River catchment as agricultural land-use exceeds 50 percent of the watershed land-use during the wet season. The variation partitioning shows that a substantial fraction of the variation is jointly explained by these two sets of variables. This fraction reflects that some land-use variables and in-stream environmental variables tend to be correlated in the field and thus their contribution to biotic responses cannot be separated. Hence it represents variation in macroinvertebrates that is explained by the variables, but we cannot statistically attribute the effect to environmental or land-use variables, respectively.

Although the indicator taxon analyses showed that Baetidae and Heptageniidae were indicator taxa of good water quality conditions in both seasons, there was a substantial variation in indicator taxon between seasons. For example, Hydropsychidae and Potamonautidae showed to be an indicator taxon of good water quality conditions in the wet and dry seasons respectively. Several studies have shown that Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa are sensitive to pollution (Rosenberg and Resh, 1993; Barbour et al., 1999; Soininen and Kononen, 2004; Masese et al., 2009; Al-shami et al., 2011). Therefore, their presence is often an indication of good water quality conditions, similar to the present study findings. A study of Kaaya et al. (2015), however, indicated Potamonautidae to be tolerant of pollution with a lower TARISS score, while we found them to be indicative of good water quality conditions. This family likely comprises both pollution tolerant and sensitive species. Judging water quality in the region based on the presence of members of this family is therefore not possible unless differential responses of genera and species within this family are known. Chironomidae was an indicator of poor water quality conditions in the wet season while Hirudinea showed to be indicator taxa of poor water quality condition in the dry season. When streams are disturbed, taxa that are sensitive to pollution will be eliminated, leaving communities to be dominated by only taxa that are resistant (i.e., able to survive the impacts) or resilient (i.e., having efficient recovery mechanisms). Chironomids, for example, are capable of surviving low dissolved oxygen levels and high turbidity and can exploit excess nutrients, hence dramatically increase in abundance in polluted water (Marques et al., 1999; Özkan et al., 2010). This explains why they appear as indicator taxa in the wet season but not in the dry season, when nutrients and turbidity are not an issue.

The macroinvertebrate biotic index developed for Tanzania (i.e. TARISS) was shown to be a complementary source of information compared to richness and analyses of composition. In the predictive model, TARISS was significantly affected by several variables that had no effects on richness.

Hence, it does what it was intended for: providing a metric that integrates both richness and known sensitivity of taxonomic groups. A limitation of this study is that only two seasons were studied and, although they were quite representative in terms of typical weather conditions, longer-term monitoring would be required to validate to what extent the reported dynamics are indeed general. It would also be valuable to know to what extent water quality responds to particularly dry or wet years and to what extent variation in agricultural runoff among years has strong effects on biota.

The study highlights that current agricultural practices are indeed in all likelihood affecting the macroinvertebrate assemblages in this river and that monitoring them via their indicator species may help to identify sites with poor water quality where remediation actions can be taken. Riparian buffer zones may help to alleviate some of the observed negative effects of agricultural activities on the river system in the wet season while limiting irrigation return flows may improve water quality in the dry season. In addition, macroinvertebrate monitoring may also help to detect effects of extreme weather events expected under current scenarios of global climate change. Many perennial rivers are likely to be become non perennial and this risk also exists for the Ruvu river catchment. During the dry parts of the year some sections of the river no longer have flowing water with stagnant pools remaining with poor water quality. In fact, many rivers in the area currently suffer potential degradation due to increased water abstraction, nutrient enrichment and siltation resulting from land-use change mainly for agricultural activities and settlement. The combination with climate change may lead to further deterioration of water quality with serious consequences for the growing population that is predominantly reliant on river water as drinking water and for irrigation purposes.

In conclusion, the study generated some new generic insights into the ecology of this type of tropical rivers by showing that different indicator species as well as different drivers of water quality and macroinvertebrates can be important during dry and wet seasons. Using a combined multivariate approach of indicator species analysis and biological indices allowed a more profound ecological diagnosis of the ecological condition of the Ruvu River and (re)confirmed the usefulness of benthic macroinvertebrates in monitoring schemes of river systems. Overall, this study advocates for a reinstatement of an effective nation-wide river monitoring system in Tanzania with monitoring taking place both in the dry and in the wet season. In addition, the poor current state of many river sites urges for the development of awareness programs coupled to possible financial compensations for farmers to reduce surface runoff via the establishment of effective riparian buffer zones.

References

Akaike, H., 1974. A New Look at the Statistical Model Identification. IEEE Trans. Automat. Contr. AC-19, 716–723.

Allan, D.J., Castillo, M.M., 2007. Stream Ecology: Structure and Functioning of Running Waters, Second Edi. ed. Springer Netherlands.

Allan, J.D., 2004. Landscapes and Riverscapes : The Influence of Land Use on Stream Ecosystems. Annu.Rev.Ecol.Syst 35, 257–84.

Al-shami, S.A., Rawi, C.S., Ahmad, A.H., Hamid, S.A., Nor, S.M., 2011. Influence of agricultural , industrial , and anthropogenic stresses on the distribution and diversity of macroinvertebrates in Juru River Basin ,Penang,Malaysia. Ecotoxicol. Environ. Saf. 74, 1195–1202.

APHA, 2012. Stand Methods for Examination of Water and Waste water, 22nd ed. ed. American Public Health Association,American Water Works Association,Water Environmental Federation, Washington, DC.

Aschalew, L., Moog, O., 2015. Benthic macroinvertebrates based new biotic score “ ETHbios ” for assessing ecological conditions of highland streams and rivers in Ethiopia. Limnologica 52, 11–19.

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid Bioassessment Protocols For Use in Streams and Wadeable RiversWadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish. Second Ed. EPA 841-B-99-002. U.S. Environ. Prot. Agency; Off. Water; Washington, DC, USA. Brewin.

Bellinger, B.J., Cocquyt, C., O’Reilly, C.M., 2006. Benthic diatoms as indicators of eutrophication in tropical streams. Hydrobiologia 573, 75–87. h

Belmar, O., Velasco, J., Gutiérrez-Cánovas, C., Mellado-Díaz, A., Millán, A., Wood, P.J., 2013. The influence of natural flow regimes on macroinvertebrate assemblages in a semiarid Mediterranean basin. Ecohydrology 6, 363–379.

Bere, T., Chiyangwa, G., Mwedzi, T., 2016. Effects of land-use changes on benthic macroinvertebrate assemblages in the tropical Umfurudzi River , Zimbabwe. African J. Aquat. Sci. 5914, 1–5.

Bere, T., Nyamupingidza, B.B., 2014. Use of biological monitoring tools beyond their country of origin: A case study of the South African Scoring System Version 5 (SASS5). Hydrobiologia 722, 223–232.

Beyene, A., Legesse, W., Triest, L., Kloos, H., 2009. Urban impact on ecological integrity of nearby rivers in developing countries: The Borkena River in highland Ethiopia. Environ. Monit. Assess. 153, 461–476.

Blanchette, M.L., Pearson, R.G., 2013. Dynamics of habitats and macroinvertebrate assemblages in rivers of the Australian dry tropics. Freshw. B 58, 742–757.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R, Springer Science+Business Media, LLC.

Botwe, P.K., Barmuta, L.A., Magierowski, R., McEvoy, P., Goonan, P., Carver, S., 2015. Temporal Patterns and Environmental Correlates of Macroinvertebrate Communities in Temporary Streams. PLoS One 1–19.

Boulton, A.J., Boyero, L., Covich, A.P., Dobson, M., Lake, S., Pearson, R., 2008. Are Tropical Streams Ecologically Different from Temperate Streams?, in: Tropical Stream Ecology. pp. 257–284.

Boyer-Rechlin, N.J., Bruland, G.L., Rechlin, M.A., 2016. The Effects of agricultural land use on benthic macroinvertebrate communities and the applicability of family level bioassessment metrics in Southern Illinois headwater streams. Trans. Illinois State Acad. Sci. 109, 49–56.

Brooks, A.J., Haeusler, T.I.M., Reinfelds, I., Williams, S., 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. Freshw. Biol. Biol. 50, 331–344. h

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information, Theoretic Approach. Springer Science & Business Media.

Chakona, A., Phiri, C., Magadza, C.H.., Brendonck, L., 2008. The influence of habitat structure and flow permanence on macroinvertebrate assemblages in temporary rivers in northwestern Zimbabwe. Hydrobiologia 607, 199–209.

Ciutti, F., Cappelletti, C., Monauni, C., Siligardi, M., 2004. Influence of Substrate Composition and Current Velocity on Macroinvertebrates in a Semi-Artificial System 19, 455–460.

Collier, K.J., 2008. Temporal patterns in the stability , persistence and condition of stream macroinvertebrate communities : relationships with catchment land-use and regional climate. Freshw. Biol. 53, 603–616.

Croft, P.S., 1986. A Key to the Major Groups of British Freshwater Invertebrates. Rep. Pub. FSC. 1986.

Dallas, H., Kennedy, M., Taylor, J., Lowe, S., Murphy, K., 2010. SAFRASS : Southern African River Assessment Scheme WP4 : Review of existing biomonitoring methodologies and appropriateness for adaptation to river quality assessment protocols for use in southern tropical Africa.

Dallas, H.F., 2004. Seasonal variability of macroinvertebrate assemblages in two regions of South Africa : implications for aquatic bioassessment. African J. Aquat. Sci. 29, 173–184.

Dallas, H.F., 1995. An Evaluation of SASS (South African Scoring System) as a Tool for the Rapid Bioassessment of Water Quality. University of Cape Town (UCT), South Africa.

Dalu, T., Froneman, W.P., 2016. Diatom-based water quality monitoring in southern Africa : challenges and future prospects. Water SA 42, 551–559.

Dalu, T., Wasserman, R.J., Magoro, M.L., Mwedzi, T., Froneman, W.P., Weyl, O.L.F., 2017a. Variation partitioning of benthic diatom community matrices : Effects of multiple variables on benthic diatom communities in an Austral temperate river system. Sci. Total Environ. 601-602, 73–82.

Dalu, T., Wasserman, R.J., Tonkin, J.D., Alexander, M.E., Dalu, M.T.B., Motitsoe, S.N., Manungo, K.I., Bepe, O., Dube, T., 2017b. Assessing drivers of benthic macroinvertebrate community structure in African highland streams : An exploration using multivariate analysis. Sci. Total Environ. 601-602, 1340–1348.

Davies, B., Day, J., 1998. Vanishing Waters: Keys to common macroinvertebrate taxa of South African Inland Waters.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684.

Dickens, C.W., Graham, P.M., 2002. The South African Scoring System (SASS) Version 5 Rapid Bioassessment Method for Rivers. African J. Aquat. Sci. 27, 1–10.

Dlamini, V., Hoko, Z., Murwira, A., Magagula, C., 2010. Response of aquatic macro-invertebrate diversity to environmental factors along the Lower Komati River in Swaziland. Phys. Chem. Earth 35, 665–671.

Dodds, W.K., Perkin, J.S., Gerken, J.E., 2013. Human Impact on Freshwater Ecosystem Services: A Global Perspective. Environ. Sci. Technol. 47, 9061−9068.

Dudgeon, D., 2010. Prospects for sustaining freshwater biodiversity in the 21st century : linking ecosystem structure and function. Curr. Opin. Environ. Sustain. 2, 422–430.

Dudgeon, D., 2008. Tropical Stream Ecology; Academic Press: London, UK, 2008.

Dudgeon, D., 1992. Endangered ecosystems: a review of the conservation status of tropical Asian rivers: Hydrobiologia 248(3), 167–191.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z., Naiman, R.J., Knowler, D.J., Leveque, C., Soto, D., Prieur-Richard, A.-H., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity : importance , threats , status and conservation challenges. Biol. Rev. 81, 163–182.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Elias, J.D., Ijumba, J.N., Mgaya, Y.D., Mamboya, F.A., 2014. Study on Freshwater Macroinvertebrates of Some Tanzanian Rivers as a Basis for Developing Biomonitoring Index for Assessing Pollution in Tropical African Regions. J. Ecosyst.

Fugère, V., Kasangaki, A., Chapman, L.J., 2016. Land use changes in an afrotropical biodiversity hotspot affect stream alpha and beta diversity. Ecosphere 7, 1–18.

Genito, D., Gburek, W.J., Sharpley, A.N., 2002. Response of Stream Macroinvertebrates to Agricultural Land Cover in a Small Watershed. J. Freshw. Ecol. 17, 109–119.

Gerber, A., Gabriel, M.J.M., 2002. Aquatic Invertebrates of South African Rivers: Field Guide. Institute for Water Quality Studies.

Harding, J.S., Young, R.G., Hayes, J.W., Shearer, K.A., Stark, J.D., 1999. Changes in Agricultural Intensity and River Health Along a River Continuum. Freshw. Biol. 42, 345–357.

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

Hering, D., Johnson, R.K., Kramm, S., Schmutz, S., Szoszkiewicz, K., Verdonschot, P.F.M., 2006. Assessment of European streams with diatoms , macrophytes , macroinvertebrates and fish : a comparative metric-based analysis of organism response to stress. Freshw. Biol. 51, 1757–1785.

Hrodey, P.J., Sutton, T.M., Frimpong, E.A., 2009. Land-Use Impacts on Watershed Health and Integrity in Indiana Warmwater Streams. Am. Midl. Nat. 16, 76–95.

IUCN Eastern Africa Programme, 2003. The Pangani River Basin : A Situation Analysis.

Jun, Y., Kim, N., Kim, S., Park, Y., Kong, D., 2016a. Spatial Distribution of Benthic Macroinvertebrate Assemblages in Relation to Environmental Variables in Korean Nationwide Streams. Water 8, 1–20.

Jun, Y., Kim, N., Kim, S., Park, Y., Kong, D., Hwang, S.-J., 2016b. Spatial Distribution of Benthic Macroinvertebrate Assemblages in Relation to Environmental Variables in Korean Nationwide Streams. Water 8, 1–20.

Kaaya, L.T., 2014. Biological Assessment of Tropical Riverine Systems Using Aquatic Macroinvertebrates in Tanzania, East Africa. University of Cape Town, South Africa.

Kaaya, L.T., Day, J.A., Dallas, H.F., 2015. Tanzania River Scoring System (TARISS): a macroinvertebrate-based biotic index for rapid bioassessment of rivers. African J. Aquat. Sci. 40, 109–117.

Kalkhoff, S.J., Hubbard, L.E., Tomer, M.D., James, D.E., 2016. Effect of variable annual precipitation and nutrient input on nitrogen and phosphorus transport from two Midwestern agricultural watersheds. Sci. Total Environ. 559, 53–62.

Karaouzas, I., Gritzalis, K.C., Skoulikidis, N., 2007. Land Use Effects on Macroinvertebrate Assemblages and Stream Quality Along an Agricultural River Basin. Fresenius Environ. Bull. 16, 645–653.

Kihampa, H.H., De Wael, K., Lugwisha, E., Van Grieken, R., 2013. Water quality assessment in the Pangani River basin, Tanzania: natural and anthropogenic influences on the concentrations of nutrients and inorganic ions. Int. J. River Basin Manag. 11, 55–75.

Kilonzo, F., Masese, F.O., Van Griensven, A., Bauwens, W., Obando, J., Lens, P.N.L., 2014. Spatial-temporal variability in water quality and macro-invertebrate assemblages in the Upper Mara River basin, Kenya. Phys. Chem. Earth 67-69, 93–104.

Kiptala, J.K., Mohamed, Y., Mul, M.L., Cheema, M.J.M., Van Der Zaag, P., 2013. Land use and land cover classification using phenological variability from MODIS vegetation in the Upper Pangani River Basin, Eastern Africa. Phys. Chem. Earth 66, 112–122.

Klein, I., Gessner, U., Kuenzer, C., 2012. Regional land cover mapping and change detection in Central Asia using MODIS time-series. Appl. Geogr. 35, 219–234.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Legendre, P., Lengendre, L., 2012. Numerical Ecology. 2nd English Edition. Elsevier Science, Amsterdam, Netherlands.

Li, F., Chung, N., Bae, M., Kwon, Y., Park, Y., 2012. Relationships between stream macroinvertebrates and environmental variables at multiple spatial scales. Freshw. Biol. 57, 2107–2124.

Li, L., Zheng, B., Liu, L., 2010. Biomonitoring and Bioindicators Used for River Ecosystems : Definitions , Approaches and Trends. Procedia Environ. Sci. 2, 1510–1524.

Lumbreras, A., Marques, J.T., Belo, A.. ., Cristo, M., Fernandes, M., Galioto, D., Machado, M., Mira, A., Sá-Sousa, P., Silva, R., Sousa, L.., Pinto-Cruz, C., 2016. Assessing the conservation status of Mediterranean temporary ponds using biodiversity : a new tool for practitioners. Hydrobiologia 782, 187–199.

Magierowski, R.H., Davies, P.E., Read, S.M., Horrigan, N., 2012. Impacts of land use on the structure of river macroinvertebrate communities across Tasmania , Australia : spatial scales and thresholds. Mar. Freshw. Res. 63, 762–776.

Malmqvist, B., Rundle, S., 2002. Threats to the running water ecosystems of the world. Environ. Conserv. 29, 134–153.

Marques, M.M., Barbosa, F.A., Callisto, M., 1999. Distribution And Abundance Of Chironomidae (Diptera , Insecta) In An Impacted Watershed In South-East Brazil. Rev. Bras. Biol. 59, 553–561.

Masese, F.O., Muchiri, M., Raburu, P.O., 2009. Macroinvertebrate assemblages as biological indicators of water quality in the Moiben River , Kenya. African J. Aquat. Sci. 34, 15–26.

Masikini, R., Tunu, L., Chicharo, L., 2018. Evaluation of ecohydrological variables in relation to spatial and temporal variability of macroinvertebrate assemblages along the Zigi River – Tanzania. Ecohydrol. Hydrobiol. 18, 130–141.

Mathew, M.M., Majule, A.E., Marchant, R., Sinclair, F., 2016. Variability of Soil Micronutrients Concentration along the Slopes of Mount Kilimanjaro , Tanzania. Appl. Environ. Soil Sci. 1–7.

Mbonile, M.J., 2005. Migration and intensification of water conflicts in the Pangani Basin, Tanzania. Habitat Int. 29, 41–67.

McCord, S.B., Kuhl, B.A., 2013. Macroinvertebrate community structure and its seasonal variation in the Upper Mississippi River , USA: a case study. Freshw. Ecol. 28, 63–78.

Metcalfe, J.L., 1989. Biological Water Quality Assessment of Running Waters Based on Macroinvertebrate Communities : History and Present Status in Europe. Environ. Pollut. 60, 101–139.

Minshall, G.W., 1984. Aquatic insect substratum relationships, in: Resh, V. H.; Rosenberg, D. M. Ed. The Ecology of Aquatic insects.New York, Praeger. pp. 358–400.

Ndaruga, A.M., Ndiritu, G.G., Gichuki, N.N., Wamicha, W.N., 2004. Impact of water quality on macroinvertebrate assemblages along a tropical stream in Kenya. Afr. J. Ecol. 42, 208–216.

Nhiwatiwa, T., Dalu, T., Brendonck, L., 2017a. Impact of irrigation based sugarcane cultivation on the Chiredzi and Runde Rivers quality, Zimbabwe. Sci. Total Environ. 587-588, 316–325.

Nhiwatiwa, T., Dalu, T., Sithole, T., 2017b. Assessment of river quality in a subtropical Austral river system : a combined approach using benthic diatoms and macroinvertebrates. Appl. Water Sci. 7, 4785–4792.

Nyenje, P.M., Foppen, J.W., Uhlenbrook, S., Kulabako, R., Muwanga, A., 2010. Eutrophication and nutrient release in urban areas of sub-Saharan Africa — A review. Sci. Total Environ. 408, 447–455.

O'Hara, R.B., Kotze, D.J., 2010. Do not log-transform count data. Methods Ecol. Evol. 1, 118–122.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, H.M.H., Szoecs, E., Wagner, H., 2016. Vegan Community Ecology Package version 2.4-1.

Ollis, D.J., Dallas, H.F., Esler, K.J., Boucher, C., 2006. Bioassessment of the ecological integrity of river ecosystems using aquatic macroinvertebrates : an overview with a focus on South Africa. African J. Aquat. Sci. 2, 205–227.

Özkan, N., Moubayed-Breil, J., Çamur-Elipek, B., 2010. Ecological Analysis of Chironomid Larvae (Diptera , Chironomidae) in Ergene River Basin (Turkish Thrace). Turkish J. Fish. Aquat. Sci. 10, 93–99.

Paisley, M.F., Walley, W.J., Trigg, D.J., 2011. Identification of macroinvertebrate taxa as indicators of nutrient enrichment in rivers. Ecol. Inform. 6, 399–406.

Pan, B., Wang, Z.-Y., Li, Z.-W., Lu, Y.-J., Yang, W.-J., Li, Y., 2013. Macroinvertebrate assemblages in relation to environments in the West River , with implications for management of rivers affected by channel regulation projects. Quat. Int. 384, 180–185.

Paulo, J., Menezes, C., Fernando, L., Oliveira, C., Salla, M.R., 2019. Metrics of benthic communities and habitat quality associated to different types of land use. Eng Sanit Ambient | 24, 737–746. https://doi.org/10.1590/S1413

PBWO/IUCN, 2007. Pangani River System: State of the Basin Report 2007.Moshi, Tanzania.

Pearson, R.G., 2014. Dynamics of Invertebrate Diversity in a Tropical Stream. Diversity 6, 771–791.

Pearson, R.G., Christidis, F., Connolly, N.M., Nolen, J.A., St Clair, R.M., Cairns, A., Davis, L., 2017. Stream macroinvertebrate assemblage uniformity and drivers in a tropical bioregion. Freshw. Biol. 62, 544–558.

Perona, E., Bonilla, I., Mateo, P., 1999. Spatial and temporal changes in water quality in a Spanish river. Sci. Total Environ. 241, 75–90.

Poff, L.N., Allan, D.J., Bain, M.B., Karr, J.R., Prestegaard, K.L., Ritcher, B.D., Richard, S.E., Stromberg, J.C., 1997. The Natural Flow Regime A Paradigm for River Conservation and Restoration. Bioscience 47, 770–784.

Principe, R.E., Raffaini, G.B., Gualdoni, C.M., Oberto, A.M., Corigliano, M.C., 2007. Do hydraulic units define macroinvertebrate assemblages in mountain streams of central Argentina ? Limnologica 37, 323–336.

Qadir, A., Malik, R.N., Husain, S.Z., 2008. Spatio-temporal variations in water quality of Nullah Aik-tributary of the river Chenab, Pakistan. Environ. Monit. Assess. 140, 43–59.

R Core Team, ., 2014. R: a language and environment for statistical computing [WWW Document]. URL http://www.R- project.org/.

Resh, V.H., Norris, R.H., Barbour, M.T., 1995. Design and implementation of rapid assessment approaches for water resource monitoring using benthic macroinvertebrates. Aust. J. Ecol. 20, 108–121.

Richards, C., Haro, R.J., Johnson, L.B., Host, G.E., 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. Biol. 37, 219–230.

Richards, C., Johnson, L.B., Host, G.E., 1996. Landscape-scale influences on stream habitats and biota. Can. J. Fish. Aquat. Sci. 53, 295–311.

Rosenberg, D.M.., Resh, V.H., 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. Ecology 75, 267–268.

Sandin, L., Johnson, R.K., 2004. Local , landscape and regional factors structuring benthic macroinvertebrate assemblages in Swedish streams. Landsc. Ecol. 19, 501–514.

Schowe, K.A., Harding, J.S., 2014. Development of two diatom-based indices : a biotic and a multimetric index for assessing mine impacts in New Zealand streams. New Zeal. J. Mar. Freshw. Res. 48, 163–176.

Selemani, J.R., Zhang, J., Muzuka, A.N.N., Njau, K.N., Zhang, G., Mzuza, M.K., Maggid, A., 2017. Nutrients' distribution and their impact on Pangani River Basin's ecosystem – Tanzania. Environ. Technol. 702–716.

Shaghude, Y.W., 2006. Review of Water Resource Exploitation and Landuse Pressure in the Pangani River Basin. West. Indian Ocean 5, 195–207.

Shimba, M.J., Jonah, F.E., 2016. Macroinvertebrates as bioindicators of water quality in the Mkondoa River , Tanzania , in an agricultural area. African J. Aquat. Sci. 41, 453–461.

Siddig, A.A.H., Ellison, A.M., Ochs, A., Villar-leeman, C., Lau, M.K., 2016. How do ecologists select and use indicator species to monitor ecological change ? Insights from 14 years of publication in Ecological Indicators. Ecol. Indic. 60, 223–230.

Soininen, J., Kononen, K., 2004. Comparative study of monitoring South-Finnish rivers and streams using macroinvertebrate and benthic diatom community structure. Aquat. Ecol. 38, 63–75.

Søndergaard, M., Jeppesen, E., 2007. Anthropogenic impacts on lake and stream ecosystems , and approaches to restoration. J. Appl. Ecol. 44, 1089–1094.

Sporka, F., Vlek, H.E., Bulankova, E., Krno, I., 2006. Influence of seasonal variation on bioassessment of streams using macroinvertebrates. Hydrobiologia 566, 543–555.

Statzner, B., Gore, J.A., Resh, V.H., 1988. Hydraulic Stream Ecology : Observed Patterns and Potential Applications Hydraulic stream. J. North Am. Benthol. Soc. 7, 307–360.

Theodoropoulos, C., Aspridis, D., Iliopoulou-Georgudaki, J., 2015. The influence of land use on freshwater macroinvertebrates in a regulated and temporary Mediterranean river network. Hydrobiologia 751, 201–213.

UNDP, 2014. Reducing Land Degradation on the Highlands of Kilimanjaro Region. Dar es Salaam, Tanzania.

Vörösmarty, C.J., Mcintyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Vo, C.J., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561.

Wilcoxon, F., 1945. Individual Comparisons by Ranking Methods. Biometrics Bull. 1, 80–83.

Zhang, Y., Wang, B., Han, M., Wang, L., 2012. Relationships between the seasonal variations of macroinvertebrates, and land uses for biomonitoring in the Xitiaoxi River watershed,China. Int. Rev. Hydrobiol. 97, 184–199.

Zuur, A.K., Ieno, E.N., Smith, G.M., 2007. Analysing Ecological Data. Springer + Business Media,LLC,Sring Street, New York,NY 10013,USA.

Supplementary Information to Chapter 1

Table S1 Descriptions of monitoring sites in the Ruvu River catchment. Abbreviations: RV=Ruvu River, RD=Dehu River, RS=Soko River and RH=Ghona River

Monitoring sites	**Sites description and land-use in its immediate catchment area**
RV1	Ruvu River at swamp. Aquatic macrophytes composed of reeds and sedges. Nearby land use consists of agriculture (sugar cane, tomatoes, bananas and vegetables), settlement and stone mining. Small scale fishing; using hooks and traditional fishing gears is carried out in this river zone
RV3	Ruvu River at Kifaru bridge. Macroinvertebrate biotope was macrophytes. Illegal sand mining along the riverbanks. Anthropogenic activities such as washing, and bathing are executed inside the river channel. Human settlement in the nearby catchment area.
RV5	Ruvu River at Kifaru Primary school. Agricultural activities (maize, beans, and vegetables) on the right side of the riverbank. Human washing and bathing, and livestock watering direct in the river. Sand biotope for macroinvertebrate sampling
RV6	Ruvu at Kitopeni village. Sedges, reeds and shrubs form the riparian vegetation within one meter. Agricultural activities in both sides of the river (growing vegetables, maize, beans, cassava, onions, tomatoes and beans). Water abstraction for irrigation using pumping machines. Macroinvertebrate biotope was sand
RV7	Ruvu River at Kitopeni Primary, downstream the confluence of Ruvu and Dehu. The water is very mucky. Cattle drinking directly into the river. Devoid of riparian vegetation. Maize, beans tomatoes are grown on the right side of the river.
RV8	Ruvu River upstream the confluence of Dehu and Ruvu River. Sedges form the riparian vegetation. Small scale agriculture (maize, tomatoes and vegetables) carried out in the nearby area (along the riverbanks), and small-scale fishing using traditional gear
RV9	Ruvu River at Tingatinga gauging station. Old railway bridge. Shrubs forms the riparian vegetation. Sand and mud biotope for macroinvertebrate sampling. Agricultural activities; growing of maize, beans, tomatoes, and vegetables
RV10	Ruvu River at Handeni village. Ther river winds up before entering Nyumba ya Mungu dam. The river channel is modified by water abstraction for irrigation. Anthropogenic activities including washing, bathing and livestock watering occurring in the river channel. Oil spill from water pump generator enters the river system.
RD1	Dehu River at Miwareni. River originates as form of small springs from the Miware forest. Nearby land-use includes the settlement (village and school), and large-scale maize, beans onion and tomato farming. The biotope for macroinvertebrate sampling is sand.
RD2	Dehu River at below TPC water intake. Large water abstraction for irrigation in the TPC sugarcane plantations. Livestock watering inside the river. Agricultural activities include growing of maize, beans, tomatoes, onions, vegetables and livestock keeping. Sand and mud form the biotope for macroinvertebrate sampling.

RD3	Dehu River at Soko Village. Encroachment of the riverbanks by agricultural activities. The water is very mucky. Intensive growing of tomatoes, beans, maize, and vegetables in the surrounding area. Mud biotope for macroinvertebrate sampling.
RD4	Dehu River at Chakindo above the confluence with Ruvu river. Shrubs and sedges form the riparian vegetation. Water is very mucky. Mud biotope for macroinvertebrate sampling. Small scale agriculture; growing of tomatoes, beans, onions and vegetables. Small scale fishing using traditional gears.
RS1	Soko River at the source. The water is used for domestic purpose such as washing, bathing and drinking. Sand biotope for macroinvertebrate sampling. Nearby land-use agriculture, settlement and protected forest
RS3	Soko River at Soko village. Intensive farming of rice, maize and tomatoes. Riparian vegetation is composed of banana plantations and shrubs. Macroinvertebrate biotope mixture of sand and mud.
RS4	Soko River upstream the confluence with Dehu River. Riverbanks devoid of vegetation cover. Mud biotope for macroinvertebrate sampling.
RH2	Ghona River at Otomero village. Riparian vegetation mixture of trees and shrubs. In stream gravel covered in silt. Nearby land-use comprises of agriculture and settlement.
RH3	Ghona River at Otomero village. Riparian vegetation mixture of trees and shrubs. Instream substrate mixture of cobbles and gravel. Nearby land-use consists of settlement and agriculture. Stone mining in the right side of the river.
RH4	Ghona River at Himo bridge. Land-use includes settlement, local brewing industry and dumping site. Instream substrate consist of cobbles, gravels and boulders.
RH5	Ghona river at Mjema. Riverbanks are well protected with minimal human impact. Instream substrate include cobbles and boulders. Nearby land-use includes agroforest and settlement
RH6	Ghona River near KINAPA get. The site is located at the right side of the Mt. Kilimanjaro Marangu get. Downstream of the Una water falls. Minimal human impact. Instream substrate include cobbles and gravels.
RH7	Ghona at Marangu. The site is located in a forested area on the foot of the Mt. Kilimanjaro with minimal human impacts. The instream substrate comprises of cobbles and gravel. Riparian vegetation composed of Afromontane forest.
RH8	Ghona River at Marangu mtoni. Well protected riverbanks and riparian vegetation. Nearby land-use includes roads, settlement and Mt. Kilimanjaro forest reserve. Instream substrate comprise of cobbles and gravels.
RH9	Ghona River downstream of Zambia waterfalls. Minimal human impacts. Instream substrate comprise of cobbles, boulders and gravels. Agroforest subsistence agriculture and settlement are land-use in the nearby catchment area.
RH10	Ghona River at Makami juu. Located in a forested area with minimal human impacts. Riparian vegetation is composed of different species of Mt. Kilimanjaro Afromontane forest.
RH11	Ghona Rive at Mshiri. The most upstream site located in a forested area with minimal human impacts. The instream substratum includes the mixture of cobbles, gravel, bedrock and boulders.

RH12	Ghona River upstream of the Kilema bridge. Instream substrate include the mixture of cobbles and gravels. Minimal human impact. Well protected riverbanks. Nearby land-use; agroforest subsistence agriculture and settlement.
RH13	Ghona River upstream of Makoa bridge. Instream substrate the mixture of cobbles and gravels. Road, scattered settlement, forest, and subsistence agriculture forms the land-use in the nearby catchment area.
RH14	Ghona River upstream of Rua bridge. Nearby land-use; agroforest subsistence agriculture, road, forest, and settlement. Instream substratum include the mixture of cobbles, gravel, bedrock and boulders.
RH15	Ghona River upstream of Zambezi bridge. Minimal human impacts Nearby land-use; agroforest subsistence agriculture, road, forest, and settlement. Instream substratum include the mixture of cobbles, gravel, bedrock and boulders.

Table S2 Description of seven land-use classes in the Ruvu River Catchment

Land-use class	**Description**
Forest	Land with natural tree canopy cover of more than 10 percent
Water Bodies	Permanent water body such as rivers and lakes
Wetland and Swamps	Natural area covered with water and aquatic vegetation
Agricultural land	Land devoted to agriculture
Agroforestry	Land dominated by mixer of crops such as banana and coffee and natural tree canopy cover
Shrub land	Areas having plant community dominated with grasses, shrubs and small trees
Bare land	Areas with bare land mixed with scattered vegetation (Klein et al., 2012)

Table S3 Summary statistics (Mean ± SD) of the physico-chemical water quality variables measured along the Ruvu River catchment (n = 4) [a] in the dry and wet seasons. Abbreviations: EC=electric conductivity, DO = dissolved oxygen, Chl-a=Chlorophyll-a, Turb=turbidity, Fluor=fluoride, NH4=ammonium, NO_3=nitrate, PO_4^{3-} = orthophosphate, TP=total phosphorus, Temp= temperature, TN=total nitrogen, COD=chemical oxygen demand, RV=Ruvu River, RD=Dehu River, RS=Soko River and RH=Ghona River

Monitoring sites	**Parameters**												
	pH	**EC µS/cm**	**DO mg/L**	**Chl_a µg/L**	**Turb ftu**	**Fluor mg/L**	**NH4 mg/L**	**NO_3^- mg/L**	**PO_4^3 mg/L**	**TP mg/L**	**TN mg/L**	**COD mg/L**	**Temp °C**
RV1	7.62±0.28	1286±46.67	1.40±0.46	171.17±120.46	0.86±1.22	0.46±0.17	0.74±0.29	1.45±1.77	1.19±1.08	4.24±3.68	1.75±1.20	78±41.01	24±1.56
RV3	7.76±0.49	1070±404.47	1.69±0.52	91.70±27.36	21.28±22.22	0.34±0.05	0.43±0.11	1±0.99	0.82±0.84	2.2±1.77	2±1.27	39±29.69	23±1.78
RV5	7.7±0.37	1085.5±376.89	2.31±0.76	108.03±51.22	11.46±10.43	0.34±0.05	0.29±0.08	1.15±1.06	0.76±0.47	2.58±2.079	2±0.14	47.5±36.06	25.5±0.5
RV6	7.76±0.36	1043±383.25	3.31±0.58	107.68±62.89	8.18±0.47	0.34±0.03	0.52±0.25	0.45±0.35	0.52±0.42	1.43±1.30	1.8±1.69	35.2±17.25	25.7±1.2
RV7	7.94±0.22	965.5±159.10	4.53±0.71	105.11±62.92	29.64±28.79	0.32±0.09	0.35±0.07	1.15±0.78	0.72±0.78	1.82±1.51	1.55±1.77	36.5±24.75	21.6±0.8
RV8	7.75±0.11	1045.5±382.55	4.51±0.12	112.35±68.17	8.45±0.83	0.36±0.04	0.48±0.28	0.7±0.42	0.57±0.45	1.65±1.32	1.75±0.63	32.4±20.36	27.1±1.1
RV9	7.9±0.57	939±165.46	5.22±1.12	116.97±63.41	54.87±60.29	0.34±0.10	0.13±0.13	0.95±0.64	0.78±0.7	1.95±1.13	1.45±1.77	38±29.69	26.6±2.3
RV10	7.93±0.45	968±243.25	5.3±1.07	128.68±70.04	44.21±23.75	0.37±0.05	0.17±0.16	0.9±0.71	0.63±0.53	1.76±1.29	1.3±1.69	52±1.41	20.8±1.6
RD1	7.48±0.17	352.5±3.54	6.82±1.30	33.21±27.76	21.74±29.35	0.15±0.06	0.06±0.05	0.7±0.14	0.21±0.06	0.93±0.79	0.775±1.03	11±15.56	19.1±0.9
RD2	7.59±0.43	326±69.30	6.89±0.92	46.89±3.29	68.97±95.50	0.14±0.04	0.04±0.03	1.1±0.14	0.34±0.1	1.26±0.43	1.23±1.65	9.5±4.95	21.3±1.4
RD3	8.19±0.12	673.5±379.72	6.33±0.66	71.00±4.97	206.37±225.05	0.28±0.17	0.17±0.10	1±0.28	0.19±0.12	0.96±0.11	1.8±0.71	10.5±0.71	21.5±2.4
RD4	7.69±0.18	701.5±333.05	4.69±1.17	68.42±48.38	40.48±4.64	0.30±0.23	0.50±0.19	0.7±0.28	0.38±0.24	1.58±0.42	1.6±1.56	6.35±4.74	20.7±1.5
RD5	8.34±0.11	754.5±297.70	6.73±0.23	66.93±34.80	69.69±34.39	0.33±0.16	0.21±0.18	0.45±0.21	0.41±0.05	1.42±0.25	5.3±4.38	19±16.97	24.4±0.3
RS1	7.95±0.71	426±24.04	7.65±0.91	30.28±37.08	0	0.22±0.07	0.06±0.01	1.1±0.14	0.39±0.04	0.98±0.06	2.05±0.35	1.45±0.78	17.9±0.6

RS3	8.02 ±0.28	598±1.41	5.79 ±1.47	40.06±25.05	32.41±24.16	0.26±0.06	0.11±0.08	0.45±0.07	0.47±0.05	1.07±0.04	1.05±1.35	13.5±16.26	22.7 ±1.3
RS4	8.87 ±0.56	1283±49.50	6.36 ±0.06	142.89±83.46	44.8±36.23	0.42±0.34	0.14±0.08	3.2±3.96	0.66±0.08	2.79±0.46	1.55±2.05	36±26.87	21.2 ±1.1
RS5	7.01 ±0.89	500±76.37	6.21 ±0.90	36.20±44.05	23.80±21.89	0.21±0.03	0.06±0.06	0.9	0.37±0.12	1.20±0.30	2.15±0.49	7	20.4 ±0.2
RH3	7.86 ±0.42	158±89.09	9.95 ±1.92	45.49±43.53	12.61±13.51	0.12±0.02	0.09±0.08	0.35±0.21	0.14±0.04	0.53±0.07	1.45±0.49	6±1.41	21.9 ±0.7
RH5	7.90 ±0.47	134±19.80	8.94 ±1.44	18.22±21.87	7.90±6.46	0.08±0.01	0.06±0.028	0.55±0.49	0.16±0.15	0.71±0.35	3.3±1.13	10.95±9.97	19.1 ±1
RH6	7.48 ±0.63	74.5±20.51	8.27 ±1.15	20.93±28.92	0	0.06±0.017	0.06±0.03	0.3±0.14	0.13±0.1	0.59±0.16	1.35±0.07	29.75±16.61	18.5 ±1.2
RH7	7.09 ±0.09	107.5±58.69	8.32 ±1.13	35.17±47.33	0	0.06±0.015	0.11±0.06	0.25±0.21	0.16±0.17	0.56±0.49	2.65±0.78	49.45±14.92	18.9 ±0.4
RH8	7.26 ±0.15	101.5±19.09	8.96 ±1.71	24.48±32.62	3.65±3.39	0.065 ±0.01	0.14±0.06	0.3±0.28	0.1±0.03	0.48±0.02	6.75±5.020	12.7±10.32	20.1 ±0.7
RH9	7.57 ±0.62	105±43.84	8.13 ±1.04	20.24±27.18	0	0.06±0.01	0.07±0.07	0.275 ±0.18	0.09±0.05	0.485 ±0.05	1.9±0.28	27.6±29.13	20.3 ±0.5
RH10	7.15 ±0.04	51±1.41	9.06 ±1.71	29.46±16.07	4.56±6.44	0.05±0.001	0.04±0.03	0.36±0.34	0.1±0.03	0.43±0.01	3.2±2.40	15.95±9.83	19.9 ±0.8
RH11	7.65 ±0.66	44.5±12.02	7.74 ±0.37	37.78±36.37	4.42±2.39	0.06	0.10±0.04	0.455 ±0.49	0.13±0.1	0.44±0.15	1.25±1.63	37.4±14.71	18.4 ±0.7
RH12	7.39 ±0.37	54.5±9.19	8.06 ±0.02	24.26±13.31	11.33±12.46	0.06	0.09±0.08	0.4±0.42	0.1±0.11	0.73±0.17	1.2±0.99	11.3±5.23	19.5 ±1.3
RH13	7.68 ±0.42	105±4.24	7.90 ±0.40	27.29±26.69	11.55±8.37	0.077 ±0.02	0.056 ±0.04	0.415 ±0.40	0.1±0.07	0.4±0.13	0.6±0.57	9.8±5.94	20.2 ±0.3
RH14	7.23 ±0.09	103.5±6.36	7.97 ±0.22	28.17±30.76	9.60±6.71	0.07±0.01	0.10±0.06	0.35±0.21	0.15±0.06	0.50±0.21	1.7±0.71	11.15±5.87	17.1 ±0.5
RH15	7.49 ±0.46	90±8.49	7.96 ±0.24	47.81±48.63	8.28±6.83	0.06±0.01	0.1	0.45±0.49	0.11±0.04	0.58±0.02	1.2±1.27	10.55±0.78	19.2 ±0.6

[a] n is number of water samples measured. At each monitoring site two water samples were analyzed for physico-chemical water quality parameters at each sampling occasion (dry and wet), n= (2x2).

Table S4 Macroinvertebrates assemblage along the Ruvu river catchment in the dry and wet seasons. Abbreviations: RV=Ruvu River, RD=Dehu River, RS=Soko River and RH=Ghona River

Taxa		Monitoring sites													
		RV 1	RV 3	RV 5	RV 7	RV 8	RV 9	RV 10	RD 1	RD 3	RD 4	RD 5	RS 1	RS 3	RS 4
Ephemeroptera	Baetidae	9				2	132	3	1		13		16	2	1
	Caenidae				38	5	25	1	1	1	91		34	15	7
	Heptageniidae														
	Ephemerythidae														
	Leptophlebidae														
Trichoptera	Hydropsychidae						1								
	Ecnomidae				1			1							
	Leptoceridae														
	Philopotamidae														
	Hydroptilidae														
	Psychomiidae														
Odonata	Aeshinidae						7	2							
	Libellulidae				7		5				1		3		
	Gomphidae							5						2	
	Coenagrionidae	2			3	9	95	2		3	21		18	3	1
	Chlorocyphidae												1		
Annelida	Oligochaeta	1					5						1	1	2
	Hirudinea	4	1		1										
Gastropoda	Physidae									1					
	Lymnaenidae												3	3	2
	Planorbidae	4			23		2				2		5		
	Thiaridae					1				15	2	1	1	1	
Bivalvles	Sphaeriidae														
Trombidiformes	Hydrachnidiae														
Coleoptera	Gyrinidae														
	Elmidae					4					1		3		
	Psephenidae														
	Helodidae						1								
	Hydrophilidae	1			2	1	5	1							
	Torridincolidae						1								
	Noteridae	3			1										
	Curculionidae				4										
	Dytiscidae					2									
Crustacea	Potamonautidae								1	1	1				
	Atyidae					11					58				
Diptera	Athericidae														
	Tabanidae					1									
	Culicidae					2	1								
	Chironomidae	179	442	143	68	6	88	8		14	21	12	53	6	15
	Tipulidae												1		
	Simuliidae														
	Scyomyzidae					2							1		
	Dixidae														
	Psychodidae														
	Ceratopogonidae					2	2						2		
	Empididae														
	Stratiomyidae												1		
Hemiptera	Gerridae						3								
	Veliidae					2									
	Naucoridae	4			3	17	7	2			3				
	Mesoveliidae												4		
	Pleidae					1	9								
	Nepidae										2				
	Hebridae				1		72						13		
	Belostomatidae									9					
	Corixidae														
Lepidoptera	Pyralidae				2								2		
Araneae	Argyronetidae	1													
Porifera	Porifera														
Plecoptera	Notonemouridae														
	Perlidae														
Tricladida	Planaridae	9		5			4								7

Taxa		Monitoring sites													
		RH 2	RH 3	RH 4	RH 5	RH 6	RH 7	RH 8	RH 9	RH 10	RH 11	RH 12	RH 13	RH 14	RH 15
Ephemeroptera	Baetidae	3	38	1	24	82	159	345	15	22	61	28	468	338	838
	Caenidae	1	69	26	15	15	4	42	6	1		2		5	245
	Heptageniidae		4	2	17	6	17	59	65	8	4	5	3	3	122
	Ephemerythidae				2		7	226				2		19	19
	Leptophlebidae		57	15					1					1	
Trichoptera	Hydropsychidae	1	1	37	8		22	274	3	1	7	15	27	14	153
	Ecnomidae		3	2			1								2
	Leptoceridae					4	5								
	Philopotamidae							2							4
	Hydroptilidae							1							1
	Psychomiidae					2		3							5
Odonata	Aeshinidae		2	2	4	4		3	1	2				6	18
	Libellulidae														
	Gomphidae	23	2						1			1			34
	Coenagrionidae					1	3								1
	Chlorocyphidae														
Annelida	Oligochaeta				2										
	Hirudinea														
Gastropoda	Physidae														
	Lymnaenidae														
	Planorbidae		1												
	Thiaridae														
Bivalvles	Sphaeriidae					8	3								
Trombidiformes	Hydrachnidiae					8									3
Coleoptera	Gyrinidae						2		2						2
	Elmidae		1	3	3	3		14				4		31	43
	Psephenidae			9	5		1	43	1		5		1	6	66
	Helodidae							2						1	69
	Hydrophilidae														1
	Torridincolidae											1			
	Noteridae														
	Curculionidae														
	Dytiscidae														
Crustacea	Potamonautidae	1		34	4	1	6	17		2	15	14	12	7	81
	Atyidae														
Diptera	Athericidae		11	7			1	4					2	1	1
	Tabanidae														
	Culicidae														
	Chironomidae	26	153	62	12	2	22	27	7	2	3	13	5	12	24
	Tipulidae			1	5		1	2				1	3	1	13
	Simuliidae	1			16	15	4	93	4	1		7	3	67	116
	Scyomyzidae														
	Dixidae												1		
	Psychodidae			1									1	2	
	Ceratopogonidae														
	Empididae		7					1	1			1	6	1	43
	Stratiomyidae														3
Hemiptera	Gerridae														
	Veliidae														
	Naucoridae						1						1		
	Mesoveliidae	3					1	2							18
	Pleidae														
	Nepidae														
	Hebridae														
	Belostomatidae														
	Corixidae														9
Lepidoptera	Pyralidae	1													1
Araneae	Argyronetidae				1				3						5
Porifera	Porifera							5							5
Plecoptera	Notonemouridae					3		5							8
	Perlidae						3		1				3	4	17
Tricladida	Planaridae														

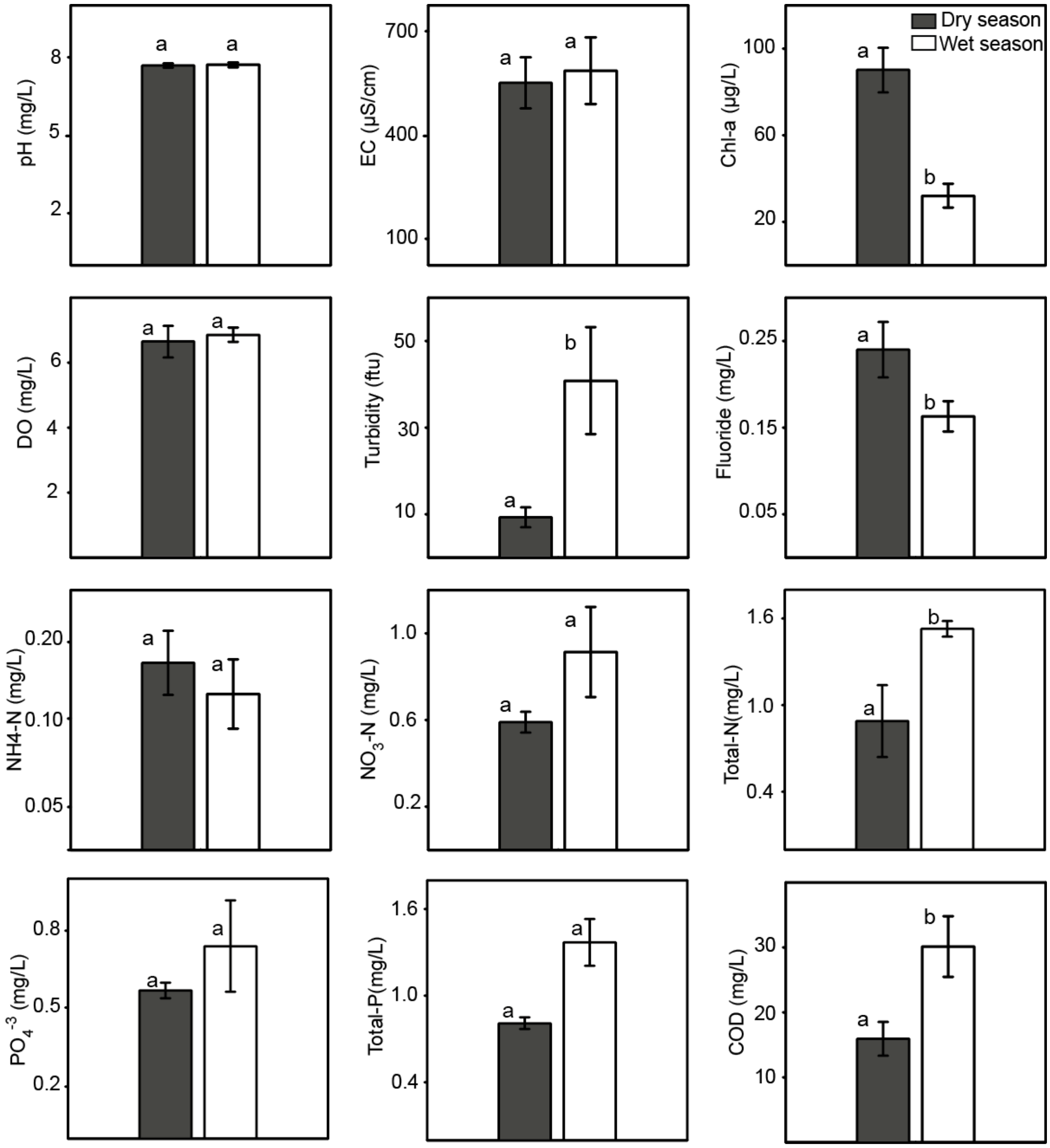


Fig. S1 Bar graphs of the seasonal variation (mean ± SE) in physico-chemical water quality variables in the Ruvu River catchment. **aa** indicates no-significant difference, and **ab** indicates significant difference based on Wilcoxon signed rank test (at $p \leq 0.05$). Abbreviations: EC=electric conductivity, Chl-a=chlorophyll-a, Turb=turbidity, DO = dissolved oxygen, PO_4^{3-}= orthophosphate, NO_3^{-}N=nitrate, NH_3-N=ammonia, TP=total phosphorus, TN=total nitrogen and COD=chemical oxygen demand.

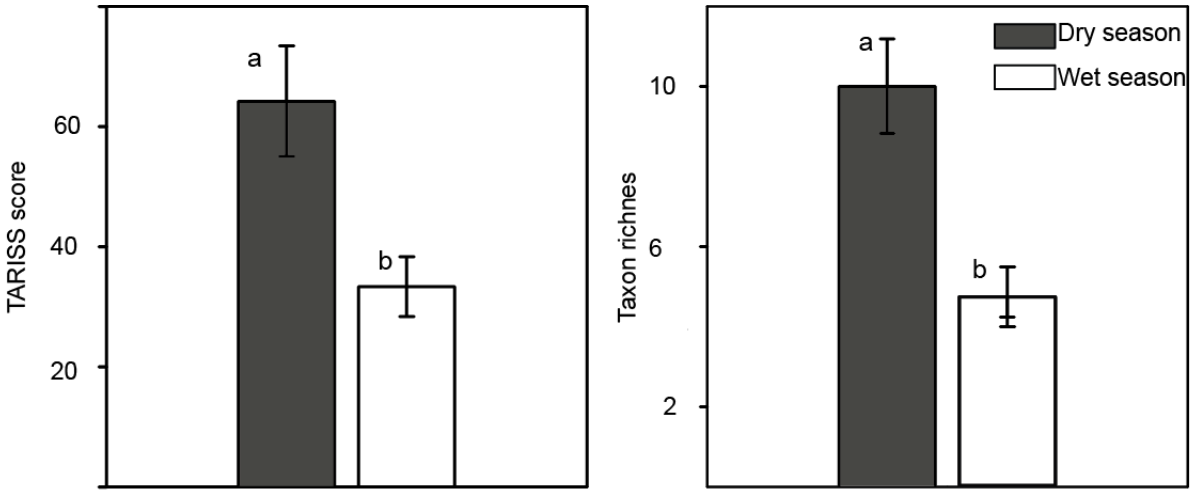
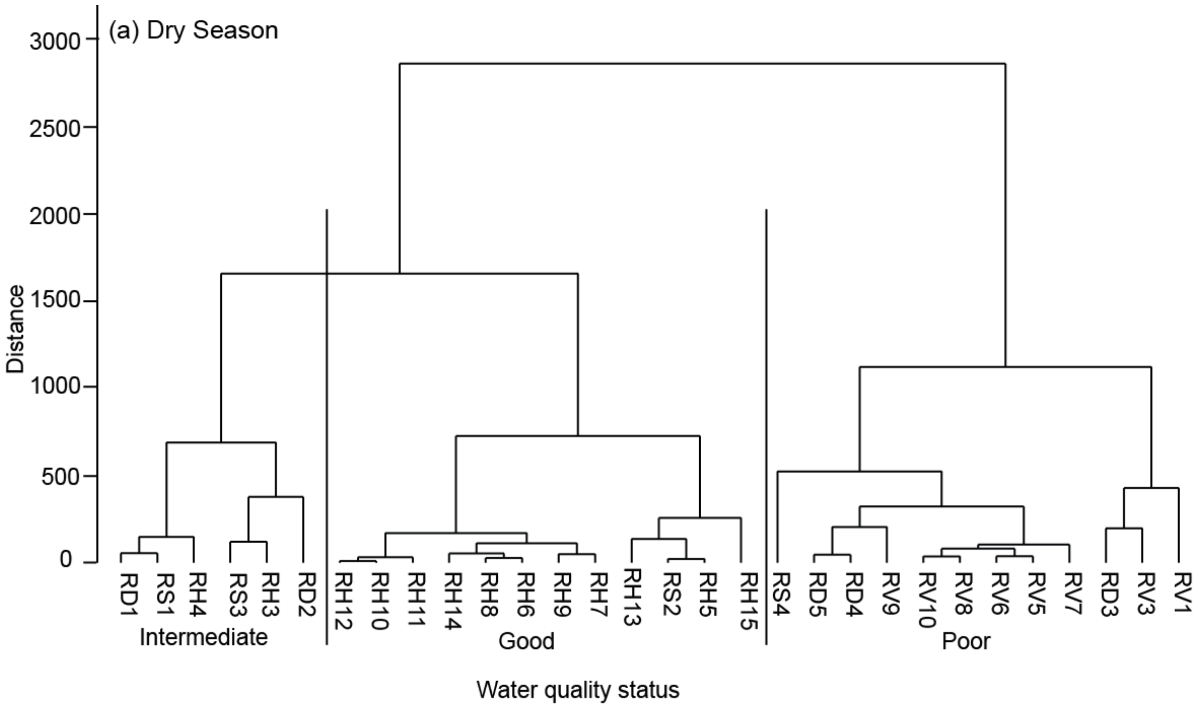


Fig. S2 Bar graphs of the seasonal variation (mean ± SE) in macroinvertebrate biotic indices in the Ruvu River catchment. **ab** indicates significant difference based on Wilcoxon signed rank test (at $p \leq 0.05$). TARISS=Tanzania River scoring system.



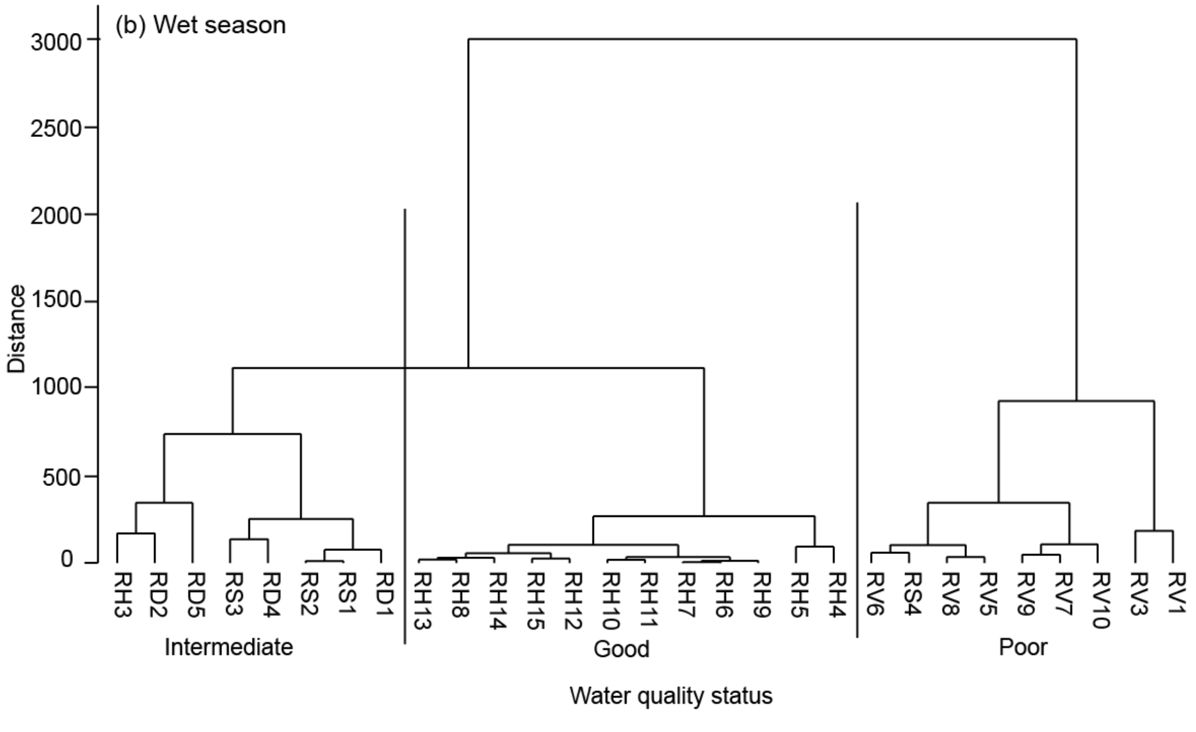


Fig. S3 Cluster diagram (Ward's method) based on TARISS scores showing the water quality statuses in the Ruvu river catchment in the (a) dry and (b) wet seasons. Abbreviation: RV= Ruvu River, RD= Dehu River, RS=Soko River and RH = Ghona River.

Chapter 2

Where Does Land Use Matter Most? Contrasting Land Use Effects on River Quality at Different Spatial Scales

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Abstract

Understanding the influence of land-use activities on river quality has been a key focus of river monitoring programs worldwide. However, defining which land-use spatial scale is relevant remains elusive. In this study, therefore, we contrasted the influence of land-use on river quality using three types of land-use estimators, namely circular buffers around a monitoring site, circular buffers upstream of the monitoring site and the entire watershed area upstream of the monitoring site. The land-use percentage compositions within the Usa-Kikuletwa River catchment in northeastern Tanzania were quantified using Landsat-8 satellite images with a maximum mapping resolution of 30m. Redundancy analysis models and generalized linear models were used to evaluate the influence of land-use on macroinvertebrate assemblages and physico-chemical water quality at different spatial scales in the dry and wet seasons. Overall, a substantial fraction of variation in physico-chemical water quality, macroinvertebrate taxon richness, Chao-1 and TARISS (Tanzania River Scoring System) score could be explained by land-use of the entire watershed area upstream of the monitoring site in the dry and wet seasons. However, macroinvertebrate abundances showed strong links with more local land-use patterns within 100m and 2km radii. Circular buffers upstream of monitoring sites were more informative for macroinvertebrate assemblages than circular buffers around the monitoring sites. However, the latter did correlate well with physico-chemical water quality variables. Land-use variables correlated across spatial scales (i.e., 100m up to 2km radii), but not with the land-use in the entire watershed area above the monitoring site. Our results indicate that physico-chemical water quality variables and macroinvertebrates may respond differently to land-uses at different scales. More importantly, our results illustrate that the choice regarding spatial land-use metrics can bias conclusions of environmental impact studies in river systems.

Keywords: circular buffers, spatial scale, macroinvertebrates, water quality, watershed

1. Introduction

Understanding the influence of anthropogenic activities on river quality (i.e., the physico-chemical and biological measure of ecological condition in the river system) has been a major focus of river water quality monitoring programs worldwide (Harding, et al., 1999; Allan, 2004; Mouri et al.,2011; Ambarita et al., 2016; Nhiwatiwa et al., 2017a). Assessing the influence of land-use and cover (henceforth termed as land-use), including vegetation cover, on river water quality has been a concern since the 1970s (Rimer et al.,1978; Shi et al. 2016). Therefore, correlating land-use with water quality is a standard approach in the field of water resources management (Kang et al., 2010). In recent decades, researchers have taken the advantage of the improvement in geographical information systems (GIS), making rapid land-use studies possible and greatly increasing the number of peer-reviewed publications reporting on the relationship between land-use variables and the physico-chemical and biological condition of river systems has increased (Morley and Karr, 2002; Allan, 2004; King et al., 2005; Schiff and Benoit, 2007; Tran et al., 2010; Stanfield and Kilgour, 2012; Ding et al., 2016).

River ecosystem dynamics are driven by multiple natural and anthropogenic factors operating at different spatial scales (Dalu et al., 2017a). Physico-chemical and biological characteristics of rivers and streams are integrally linked to watershed properties (Allan, 2004; King et al., 2005; Richards and Host, 1994; Sponseller et al., 2001; Stanfield and Kilgour, 2012). Therefore, landscape configurations play a vital role in shaping riverine conditions (Richards and Host, 1994; Richards et al., 1996). For example, riparian buffers of undisturbed vegetation are effective in reducing nutrient and sediment loading to streams and are suggested for consideration in water quality restoration programs (Meador and Goldstein, 2003; Rios and Bailey, 2006). Several studies have also shown that changes in stream hydraulics, sediment inputs, solar energy flux, and nutrient loading occur when landscapes are converted from forests and/or wetlands to agricultural and urban lands, consequently affecting assemblages and distribution of biota (Richards and Host, 1994; Dudgeon, 2000; Allan, 2004; Stanfield and Kilgour, 2012; Bere et al., 2016).

The relationships between land-use and river quality are reported to change with spatial scale, ranging from reach buffers and riparian corridors to watersheds (Allan, 2004; Sliva and Williams, 2001; Wang et al., 2014; Tonkin et al. 2015; Ding et al., 2016), but there is no consensus how. Understanding at which scale the surrounding landscape and human disturbances affect river quality at a given point is essential to adapt scale-appropriate monitoring strategies to protect and rehabilitate river ecosystems (Tudesque et al., 2014; Dalu et al., 2017a). Several studies have shown that land-use at the watershed scale strongly influences water quality (Sliva and Williams, 2001; Sponseller et al., 2001; Wang et al., 2003a; King et al., 2005; Kuemmerlen et al., 2014; Ding et al., 2016). However, other researchers have indicated that land-use activities immediately adjacent to rivers are better predictors of stream water quality conditions (Wang et al., 2003b; Schiff and Benoit, 2007; Tran et al., 2010; Stanfield and Kilgour, 2012; Shi et al., 2016). Moreover, studies that have investigated the biological responses of riverine communities to land-use at different spatial scales have produced inconsistent results. Some studies have shown that land-use at the local scale (reach or riparian scales) is a better predictor of stream community assemblage than at the watershed scale (Richards et al., 1997; Lammert and Allan, 1999; Sponseller et al., 2001; Meador and Goldstein, 2003; Strayer et al., 2003), while other studies have found that land-use at the watershed scale better accounted for variability in biotic assemblages (Roth et al., 1996; Allan et al., 1997; Young and Collier, 2009; Magierowski et al., 2012). Morley and Karr (2002) and Tudesque et al. (2014) concluded that land-use at both local and watershed scale were equally important in structuring stream biota in the Puget Sound Basin, USA and the Adour-Garonne basin, South-Western France respectively. Inconsistency in these results is likely attributed to variations in study design and differences in geographic location (Allan and Johnson, 1997; Sliva and Williams, 2001; Townsend et al., 2003; Potter et al., 2004; Schiff and Benoit, 2007). Schiff and Benoit (2007) urged that more work is needed to create a larger set of consistent results to achieve the goal of establishing land-use management strategies to protect water quality, physical habitat, and stream biotic integrity.

Studies investigating the relationships between river quality and land-use at multiple spatial scales have been conducted mainly in the temperate region (e.g., Morley and Karr, 2002; Allan, 2004; King et al., 2005; Schiff and Benoit 2007; Tran et al., 2010; Stanfield and Kilgour, 2012;Wang et al. 2014). A few studies have been conducted in the tropical region (e.g., Uriarte et al., 2011; Ding et al., 2016; Pearson et al. 2018). However, similar studies are scarce in large parts of (sub) tropical Africa, making it difficult to apply the findings from other regions given the differences in geographical location, climatic conditions, and the lack of consensus in the literature. Regional studies are needed to develop general paradigms on the multi-scale relationships between land-use and river quality. Additionally, the unique geomorphic characteristics of each river basin influence the spatial patterns of land-use and the mechanisms that link land-use to river quality (Sliva and Williams, 2001; Ding et al., 2016). Diana et al. (2006) in their study in Southeastern Michigan pointed out that land-use may play different roles in different basins, suggesting the benefit of forming separate models for individual basins when sufficient data are available. Thus, separate multi-scale analyses in each of the river basins are important for accurate assessments of land-use impacts.

While multi-spatial scale analyses of land-use impact on river quality have been conducted before, most studies have used polygon buffers (i.e., a specified width in meters on each side of a river sampling site extending a certain distance upstream) (e.g., Sponseller et al., 2001; Stanfield and Kilgour, 2012; Ding et al., 2016). Only a few studies have attempted to use an alternative method of land-use estimation (e.g., Tran et al., 2010; Magierowski et al., 2012), and most focus only on one or two spatial scales (e.g., 100m buffer and an entire watershed area). In this study, we contrast the influence of land-use on water quality and macroinvertebrate assemblages in a river network by quantifying land-use using three different spatial methods of land-use estimation: (A) land-use of the entire watershed area above the monitoring site, (B) a circular buffer around a monitoring site, and (C) a circular buffer immediately upstream of a monitoring site. Besides the entire watershed above the monitoring sites (regional scale), we used circular buffers that varied from 100m to 2km (percentage cover of different land-uses in these radii) to test for potential scale dependency of land-use effects. We used a dataset on water quality and associated benthic macroinvertebrate assemblages in the Usa-Kikuletwa River catchment in northeastern Tanzania, an important catchment in the upper Pangani River basin experiencing an increase in urbanization and agricultural activities (PBWO/IUCN, 2007a; PBWO/IUCN, 2007b). Compared to river quality assessments based on water chemistry alone, biomonitoring reflects temporal water quality changes in a more integrated manner (Dalu et al., 2017a). Benthic macroinvertebrates are commonly used for biomonitoring of river systems (Rosenberg and Resh, 1993; Barbour et al., 1999; Dickens and Graham, 2002; Hering et al., 2006; Li et al., 2010; Siddig et al., 2016). This is because they are ubiquitous and most abundant even in small streams (Rosenberg and Resh, 1993; Barbour et al., 1999), are integral components of aquatic food webs (Rosenberg and Resh, 1993; Barbour et al., 1999; Hering et al., 2006; Dalu et al., 2017b), ease to identify and rank highly as pollution-sensitive biota of river ecosystems (Dickens and Graham, 2002; Nhiwatiwa et al., 2017a).

Despite the potential of multi-scale analyses of the land-use impact on river quality, they also present certain analytical challenges. Effects of different land-use estimates on responses cannot always be isolated. When local and regional scale estimates of land-use are identical or strongly correlated, we cannot statistically distinguish at which scale land-use is most relevant. This autocorrelation is not addressed in earlier studies, but see Roth et al. (1996) and King et al. (2005) who acknowledged the problem of spatial-autocorrelation of land-use classes in watershed studies. Instead, most studies simply contrast the explanatory power of models that include local or larger scale proxies of land-use (Sponseller et al., 2001; Tran et al., 2010; Ding et al., 2016). To solve this issue, we explicitly explored the autocorrelation of land-use variables across spatial scales. In addition to the generic insights that are relevant beyond the study system, it is noteworthy that to date, multi-scale relationships between land-use and river quality in the study region have not been assessed making this information of vital importance for sustainable management of water resources in the region.

The study aimed to test which spatial method of land-use estimation and which spatial scale of land-use can best predict variation in water quality and macroinvertebrate communities in an anthropogenically modified river system. We hypothesized firstly that land-use at larger spatial scales (e.g., of the entire watershed area above the monitoring site) might explain more variation in water quality and macroinvertebrate assemblages than the land-use at small spatial scale (e.g., 100m buffer). This is likely given that the landscape is mountainous, with a lot of surface runoff, so even distant land-use activities could contribute to water quality downstream. On the other hand, local scale land-use estimates could be more informative than the watershed scale estimates, such as when localized land-use close to the river (e.g., flower farms) has larger effects on river quality via more discrete pollution. We hypothesized secondly that placement of circular buffers upstream rather than around a monitoring site might lead to better predictions given that this might better reflect the land-use of the immediate surroundings that drains towards the river monitoring site. A circular buffer around the monitoring site is less likely to contain land that drains to that particular monitoring site.

2. Materials and Methods

2.1. Study area

This study was conducted in the Usa-Kikuletwa River Catchment (Fig. 1) which is located along 36°43'0"E to 36° 57' 0" E Longitude and 3°14'0"S to 3°33'0"S Latitude in the Upper Pangani River Basin, northeastern Tanzania. The drainage area of the Usa-Kikuletwa River is about 271 km^2, and the main river channel is 40 km long. The river sources are perennial springs along the slopes of Mt. Meru (4,565 m.a.s.l.). The Usa-Kikuletwa River catchment has a semi-arid climate, with an annual mean temperature of 21 °C and average annual precipitation of approximately 2500 mm in the highlands and around 500mm in the lowland (NSCA, 2007). The catchment experiences two rainy seasons: the long rains (*masika*) from March through May and the short rains (*vuli*) which are less reliable normally coming in November and December; the dry season (*kiangazi*) is from June to October (Kiptala et al., 2013).

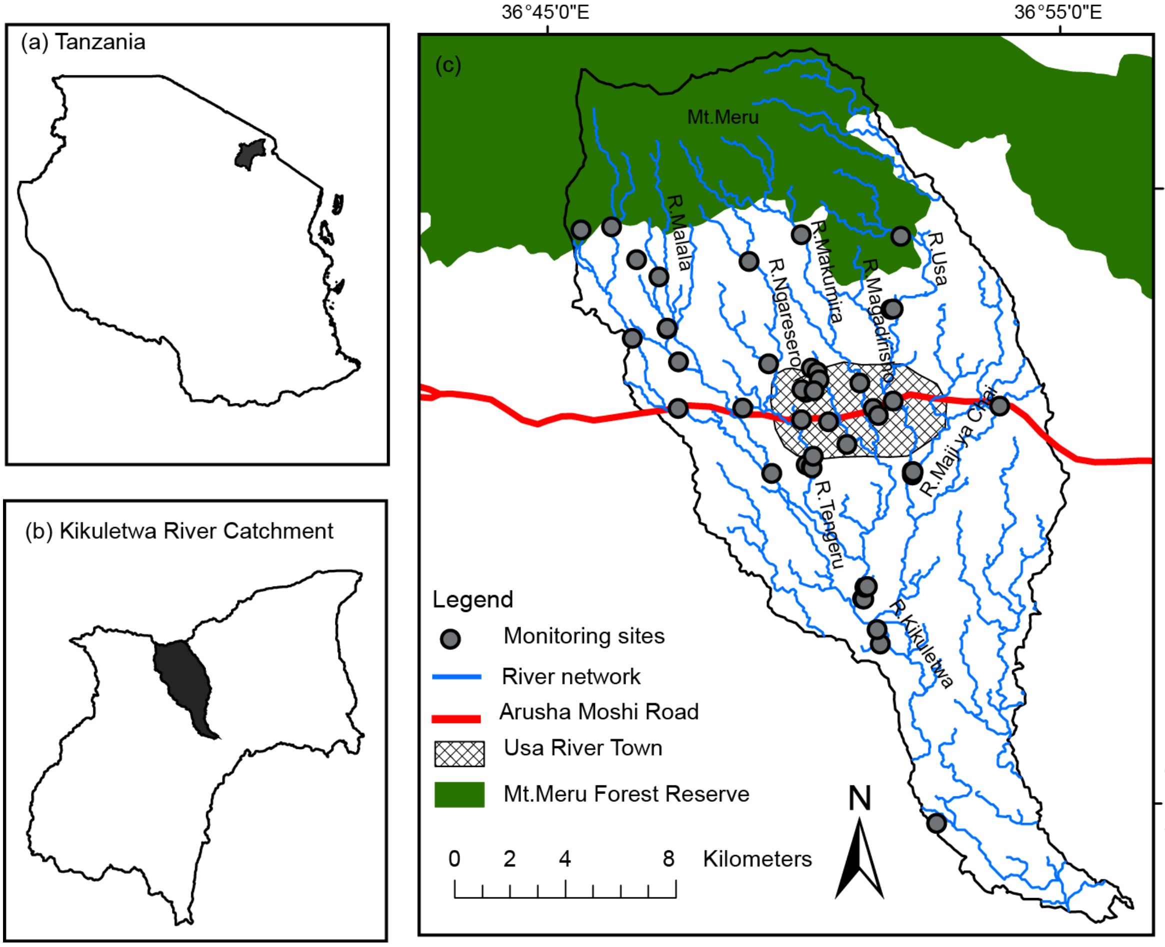

Fig.1. Map of the Usa-Kikuletwa River Catchment in northeastern Tanzania showing the location of the forty monitoring sites.

The human population of the study area is unevenly distributed, with dense populations found in the uplands because of the favorable climatic conditions and the availability of fertile soil (i.e., well-drained, dark sandy loams with high moisture-holding capacity) (Meru District Council, 2013; Elisante and Muzuka, 2016). On average the study area has a population density of 228 inhabitants per square kilometers (inhabitants per Km^2) (Meru District Council, 2013), which is four times higher than the national population density of 51 inhabitants per Km^2 (Elisante and Muzuka, 2016). Such population density is expected to have increased pressure over water resources (Elisante and Muzuka, 2016).

Agriculture and pastoralism are the primary livelihood activities in the catchment, contributing to about 70% of the household income (Meru District Council, 2013). Agroforestry and Afro-alpine forest form the dominant land-use types in the upper reaches (PBWO/IUCN, 2007b; Kiptala et al., 2013). Large scale commercial flower farming is practiced in the middle reach, which results in river water abstraction for irrigation purposes (PBWO/IUCN, 2007b). The lower reaches of the catchment wind their way through a dry landscape where the human population is sparse. Land-use is dominated by irrigation agriculture (maize, beans, rice, tomatoes, and other vegetables), shrubland and grassland (Fig.2). Free grazing is highly practiced in lower reaches, which results in overgrazing and soil erosion (Mbonile, 2005).

The study area suffers from poor sanitation and domestic waste treatment services, posing a risk to surface and ground water quality (Elisante and Muzuka, 2016). Pit latrines are the most commonly used sanitation facilities: about 80 % of households in the area use pit latrines of varying depth while others use indiscriminate sanitation including open defecation (Meru District Council 2013; Elisante and Muzuka 2016).

2.2. Study design

Forty monitoring sites were chosen in the Usa-Kikuletwa River catchment and their locations were recorded using a hand-held global positioning system (Garmin Etrex 10) (Fig.1). The sites capture the latitudinal spatial range of land-use activities from upstream to downstream. The sampled sites include seven river systems, namely Malala River, Tengeru River, Makumira River, Magadirsho River, Ngaresero River, Usa River, and Maji ya chai River which drain to form the Usa-Kikuletwa catchment.

2.3. GIS analysis

Landsat-8 satellite images (OLI/TIRS) were obtained from USGS Earth Explorer (https://earthexplorer.usgs.gov/) for August 2016 and cloud masked. Ground truthing points were mapped in August 2016. ArcGIS 10.2 desktop GIS software (ESRI Company, Redlands, California, USA) was used to determine the relative composition of land-use in the Usa-Kikuletwa catchment. A supervised classification method with a maximum likelihood algorithm in ArcMap was used to classify the land-use images in the Usa-Kikuletwa catchment. The multispectral bands of Landsat 8 were used for classification. Supervised classification is a method that uses training samples of known identity to identify the pixels of the unknown identity (Anderson et al., 1976). Pixels provided 30×30 m resolution and included information from 18 land-use classes (Figure 2 and Table S1; Supplementary Information). The overall accuracy for the image was 88.5% with a kappa coefficient of 0.87.

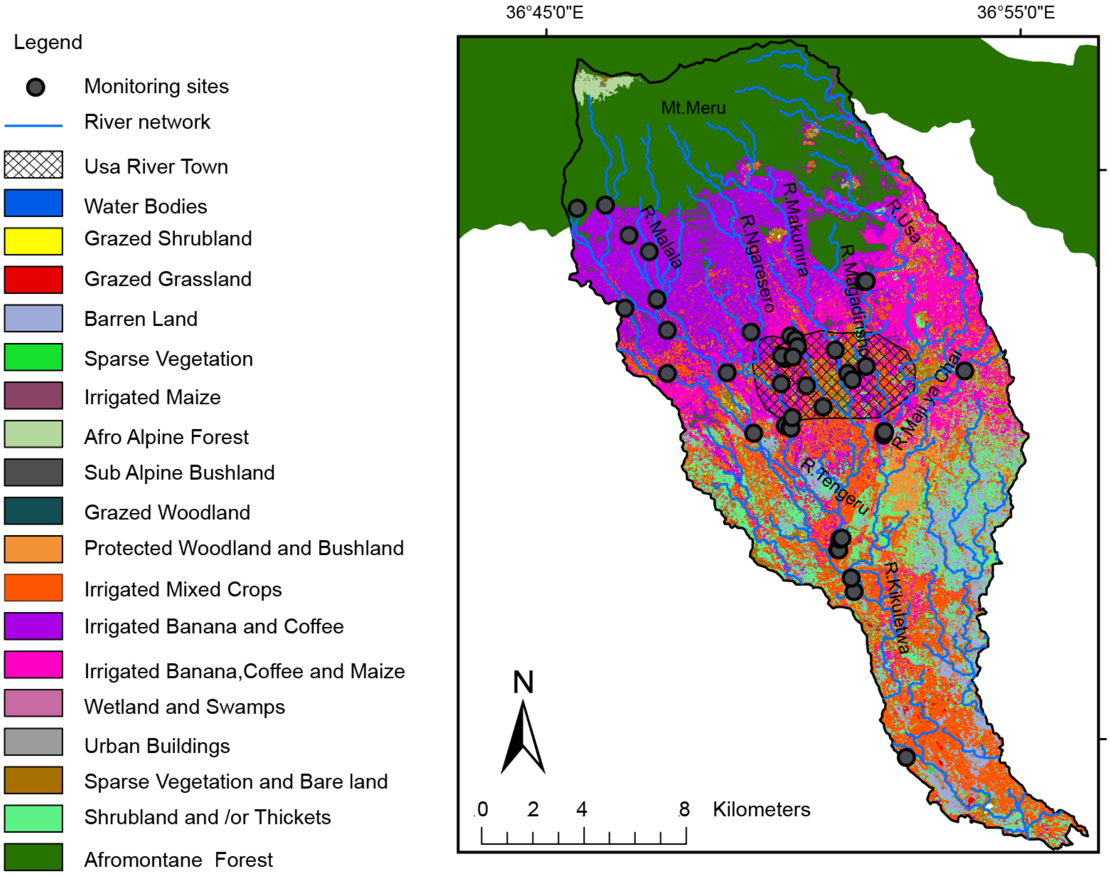

Fig. 2. Map showing the spatial distribution of eighteen different land-use classes in the Usa-Kikuletwa River catchment in relation to the river monitoring sites. (Source: Anna Msigwa)

A digital Elevation Model (DEM) (30m resolution) was used to delineate the watershed boundaries using the hydrology tools in ArcMap. Each monitoring site was treated as an outlet point. The flow-path-direction grid cells were used to delineate the upstream watershed area for each monitoring site. It should be noted that the watershed area delineated for a lower stream monitoring site encompasses the watershed corresponding to any upper stream sites. As such, the impacts of watershed land-use characteristics on the river quality at the outlet point of the watershed can be evaluated independent of the observations of adjacent monitoring sites (Kang et al., 2010). Circular buffers at different radii (i.e., 100m, 500m, 1km and 2km) around and above each monitoring site were created using geoprocessing tools (i.e., proximity tool and multiple ring buffer tool) in ArcMap (Fig.3). The radii of the analysed watershed areas ranged from 1.68 km^2 to 340.32 km^2. These buffers were overlain with a land-use layer, to create a new data layer consisting of land-use within the buffer radius. For each buffer, the land-use data were extracted using the extract by the mask tool, then the percentage land-use composition for each buffer was quantified. This procedure allowed the generation of predictor variables to test links between land-use practices at different spatial scales and water quality and macroinvertebrate assemblages for the created buffers, as well as for the whole watershed area.

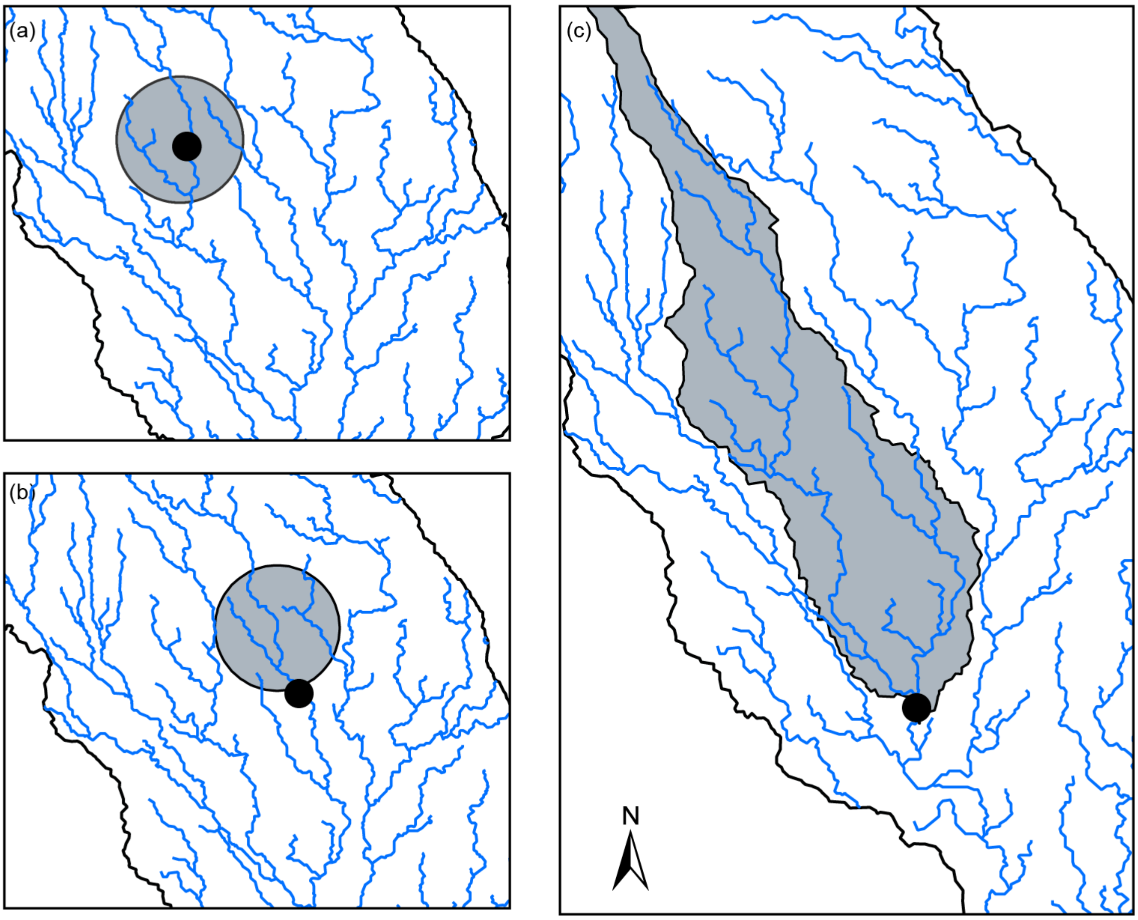

Fig.3. Hypothetical illustration of the three spatial methods of land-use estimation used to calculate land-use patterns from the monitoring sites in the Usa-Kikuletwa River catchment: (a) circular buffer around the monitoring site (b) circular buffer upstream the monitoring site, and (c) the entire watershed area upstream the monitoring site. The black dot represents a hypothetical monitoring site.

2.3. Water quality sampling and analysis

Water samples were collected from 40 monitoring sites (Fig.1) in March-April, 2016 and August-September, 2016. Two water samples were collected from each site per survey. The water samples were collected by inserting clean bottles of 1-litre at the mid-width of the river to an about 30-cm depth below the water surface in the opposite direction of the current flow of the river (APHA, 2012). The samples were transported in an iced cooler box to the laboratory of the Department of Water Environmental Science and Engineering at the Nelson Mandela African Institution of Science and Technology (NM-AIST), Arusha for analysis. The samples were stored at 4 °C until ready for analysis. Seven water quality variables: orthophosphate (PO_4^{-3}), nitrate (NO_3^--N), ammonium ($NH4^+$-N), total nitrogen (TN), total phosphorus (TP), and chemical oxygen demand (COD), which are important indicators of water pollution were chosen for measurement in the laboratory and spectrophotometrically assessed with the HACH-DR2800. Orthophosphate concentration was measured using an ascorbic acid (PhosVer 3) method (range: 0.02 to 2.50 mg/L PO_4^{3-}), nitrate concentration was measured using a cadmium reduction method (range: 0.01 to 30.0 mg/L NO_3^--N), ammonium was measured using a Nessler method (range: 0.02 to 2.50 mg/L $NH4^+$-N), total phosphorus was measured using PhosVer3 with acid persulfate digestion method (range: 0.06 to 3.50 mg/L PO_4^{3-}), total nitrogen was measured using a persulfate digestion method (range: 0.1 to 25.0 mg/L N), and chemical oxygen demand was measured using a reactor digestion method (range: 0.7 to 150.0 mg/L COD). Fluoride (F^-) was measured using an ion-selective electrode (Mettler Toledo SevenCompact™ pH/Ion S220). Conductivity (EC), pH, and dissolved oxygen (DO) were measured *in situ* using a portable HANNA multi-parameter probe (Model-HI 9829), turbidity was measured using a portable turbidity meter (HANNA-Model-HI93703), and chlorophyll-a (Chl_a) using an AquaFluor Handheld Fluorometer (Model-8000-010). Storage and chemical analyses followed the standard methods for the examination of water and wastewater by APHA (2012). The water analysis was done within 48 hours after sampling.

2.4. Macroinvertebrate sampling, identification and counting

A kick net of 1mm mesh on a 30 cm square frame was used for the collection of macroinvertebrates in a semi-quantitative way following the Tanzania River Scoring System (TARISS) method (Kaaya et al., 2015). One sample was taken at each site per sampling survey. The macroinvertebrates were sampled from the dominant habitat type at each monitoring site (i.e., the habitat that covers about 70% of the 50 m stretch making up the river section at the site). Time was used to standardize sampling effort in the stone in current habitats (a collective term for bedrock, boulders and cobbles) and gravel/sand/mud (GSM) habitats. The stones and GSM habitats were sampled for one minute. The kick-net was placed in the river in the opposite direction of current flow. Then the riverbed was agitated continuously using the sampler's feet for one minute to dislodge specimens, while continuously sweeping the net through the disturbed area to collect the macroinvertebrates. The vegetation habitat was sampled by pushing the net vigorously and repeatedly against and through the vegetation over an area of approximately two meters. All materials collected in the kick-net were transferred to a labelled collecting jar containing 70% ethanol. The jars were transported to the laboratory for sorting and identification. In the laboratory, samples were washed with tap water using a 0.5-mm mesh sieve, then transferred into a white tray to sort out all macroinvertebrate specimens before preservation in 70% ethanol. All macroinvertebrates were identified using a binocular dissecting microscope (10X magnification) to family level using three different identification guides (Croft, 1986; Davies and Day, 1998; Gerber and Gabriel, 2002).

2.5. Data Analysis

We computed descriptive statistics (minimum, mean, maximum and standard deviation) for water quality parameters and macroinvertebrate indices at each site in the dry and wet seasons. Macroinvertebrate abundances (i.e., total number of macroinvertebrates) and biotic indices: taxon richness (i.e., total number of macroinvertebrate taxa (family)), Chao-1 (i.e., Chao richness estimator for abundance data: estimation of species richness taking into account species that are not actually recorded but whose presence can be inferred from the pattern of observed species occurrence) and Tanzania River Scoring System (TARISS) (i.e., sum of the pre-determined tolerance value for each taxon per site without considering the abundance) were calculated for each monitoring site in the dry and wet seasons. The TARISS score was computed following Kaaya et al. (2015). Given that several water quality variables and biotic indices could not generate acceptable normal distributions necessary for parametric tests after transformation, we opted for the non-parametric Wilcoxon signed-rank test (Wilcoxon, 1945) at 95% confidence level to test for the significant differences in water quality variables and macroinvertebrate biotic indices between seasons. Rare species that occurred in only one monitoring site were not taken into account as they may have a disproportional impact on the analyses.

We explored to what extent land-uses at different scales generate the same statistical information. This can be the case when land-uses at a certain scale are very strongly correlated with land-use at another scale. Given that several land-use variables could not generate acceptable normal distributions necessary for Pearson correlation after transformation, we opted for the non-parametric Spearman correlation equivalent. We used Spearman correlations to explore whether land-use at scale 100m correlates with land-use at scale 200m, and so on for the circular area around, the circular area upstream, and the entire watershed above each monitoring site. For instance, we correlated percentage land-use of forest (for all sites) at the 100m scale with the same variable at the other scales. By checking the correlation coefficient (R) we can detect the extent of autocorrelation in land-use variables across scales. We judged that a Spearman R > 0.4 indicates that variables are not independent with evidence for autocorrelation, while values > 0.7 can be considered strongly autocorrelated variables (Taylor, 1990; Asuero et al., 2006). In case of strong autocorrelation in land-use across scales it is impossible to distinguish the spatial scale relevant for water quality and macroinvertebrate assemblages.

To identify the relationship between land-use variables (predictors) and water quality variables (response) at different spatial scales we constructed redundancy analysis (RDA) models (Borcard et al., 2011; Legendre and Lengendre, 2012; Shen et al., 2015; Shi et al., 2016). Separate RDA models were made using the three sets of predictor variables (i.e., circular buffer around a monitoring site, circular buffer upstream the monitoring site and entire watershed above the monitoring site) and separately for each land-use spatial scale (i.e., 100m, 500m, 1km, and 2km). We constructed separate RDA models for each season (dry and wet seasons). Similarly, the influence of land-use on macroinvertebrate abundance at different spatial scales was examined using RDA models as explained above. Prior to RDA analysis, macroinvertebrate abundance data were Hellinger transformed to improve the performance of ordination with species data (Legendre and Gallagher, 2001; Zuur et al, 2007). The significance of the RDA models was assessed using Monte-Carlo permutations (nperm= 999). A forward selection procedure was performed to retain only significant variables for each model. The models with retained significant variables were used to interpret (i) the most performant spatial method of land-use estimation (i.e., circular buffer around a monitoring site, circular buffer upstream the monitoring site or entire watershed above the monitoring site), and (ii) the relevant land-use spatial scale (i.e., 100m, 500m, 1km or 2km). The adjusted R squared coefficient (R^2_{Adj}) was used to compare model performances. The chosen best model was the one with the highest R^2_{Adj} (Legendre and Lengendre, 2012)**.**

We constructed generalized linear models with a Poisson error distribution to assess the relationships between land-use compositions and macroinvertebrate indices (i.e., taxon richness and TARISS score) for each season (dry and wet seasons). Separate generalized linear models for each macroinvertebrate index were constructed using the three sets of predictor variables (i.e., circular buffer around a monitoring site, circular buffer upstream the monitoring site and entire watershed above the monitoring site) and separately for each land-use spatial scale (i.e., 100m, 500m, 1km and 2km). For each model, a backward followed by a forward selection stepwise procedure was computed to eliminate non-significant land-use variables from the model using the step function in the vegan package (Oksanen et al., 2016). The models with retained significant variables were used to interpret (i) the most performant spatial method of land-use estimation (i.e., circular buffer around a monitoring site, circular buffer upstream the monitoring site or entire watershed above the monitoring site), and (ii) the relevant land-use spatial scale (i.e., 100m, 500m, 1km or 2km). Model performances were compared using the Akaike information criterion (AIC) and Mc Fadden's pseudo R^2 coefficient (R^2_{pseudo}). The latter is a simple measure for model fit for generalized linear models. R^2_{pseudo} coefficients are typically much smaller than conventional R^2 coefficients; values between 0.2 and 0.4 indicate an excellent model fit. AIC is an estimator of the relative quality of statistical models for a given set of data. The chosen 'best' model is the one that minimizes the Kullback-Leibler distance between the model and the data and has the lowest AIC (most parsimonious model) compared to all the other models (Burnham and Anderson, 2002).

All statistical analyses were performed in R (version 3.1. 2, R Core Team 2014) using the packages packfor, pscl, permute, and vegan.

3. Results

The descriptive statistics (minimum, maximum, mean and standard deviation) for water quality variables and macroinvertebrate indices in the Usa-Kikuletwa catchment are presented in Table 1. EC, pH, turbidity, fluoride, nitrate, chlorophyll-a, TN and TP were significantly different ($p < 0.05$) between wet and dry seasons (Table 1). High EC, fluoride, chlorophyll-a and pH levels were observed in the dry season, whereas high nutrient concentrations (TN, TP, and nitrate) and turbidity levels were observed in the wet season. A total of 13726 macroinvertebrates (abundance) consisting of 48 macroinvertebrate families (taxon richness) were recorded during the study period (Table 1). Seasonal differences ($p < 0.05$) were observed for taxon richness, TARISS score, Chao-1, and macroinvertebrate abundances. Taxon richness, Chao-1, macroinvertebrate abundances, and TARISS score were high in the dry season compared to the wet season.

Spearman's correlation coefficients (R) between land-use class percentages at different spatial scales are presented in Table S2 (Supplementary Information). Percentage land-use in 100m radii was highly correlated with land-use in 500m radii (0.4 > R < 0.8). However, the percentage land-use in 100m radii was weakly correlated with land-use in the entire watershed above the monitoring sites (average R < 0.4). The average correlation coefficient between land-use measured in 500m, 1km and 2km radii was variable (0.4 > R < 0.9). The land-use class percentages in the entire watershed above the monitoring site were weakly correlated with the same estimates measured at smaller scales (100m, 500m, and 1km) using circular buffers (average R < 0.4). The correlations between land-use classes and water quality variables and macroinvertebrate indices are presented in Tables S3 (Supplementary Information).

Table 1. Descriptive statistics and Wilcoxon signed-rank test results (indicating differences between dry and wet seasons) for water quality variables and macroinvertebrate indices in the Usa-Kikuletwa River catchment. Min=Minimum, Max=Maximum, SD = Standard deviation, z = z-statistics, *p* = p-values, EC=electric conductivity, DO=Dissolved oxygen, Turb=Turbidity, Chl_a= Chlorophyll a, TN= Total nitrogen, COD=Chemical oxygen demand, TP= Total phosphorus, Abundance= Total number of macroinvertebrates, Taxon richness= Total number of macroinvertebrate taxa (family), TARISS= Tanzania River Scoring System, Chao-1= Chao richness estimator for abundance data .Significant differences ($p < 0.05$) are highlighted in bold.

Parameter		**Min**	**Mean**	**Max**	**SD**	**Wilcoxon signed rank test**	
						z	***p***
Water quality	pH	5.80	7.78	9.53	1.05	**-4.745**	**<0.001**
	EC (µC/cm)	70	333.68	1509	246.37	**-3.357**	**<0.001**
	DO (mg/L)	4.76	6.78	9.77	0.98	-0.664	0.510
	Turb (ftu)	0	60.07	430.50	141.77	**5.012**	**<0.001**
	Fluoride (mg/L)	0.64	2.35	21.5	3.04	**4.383**	**<0.001**
	NH_3-N (mg/L)	0.03	0.08	0.54	0.11	-1.432	0.154
	NO_{3-}-N (mg/L)	0.01	0.98	4.4	0.76	**3.918**	**<0.001**
	PO_4^{3-} (mg/L)	0.13	0.46	0.96	0.22	0.887	0.379
	Chl_a (mg/L)	3.83	73.79	298.60	62.62	**-3.731**	**<0.001**
	TN (mg/L)	0.25	1.73	6.20	1.43	**2.870**	**0.004**
	COD (mg/L)	0.9	14.15	42.40	10.40	-0.821	0.415
	TP (mg/L)	0.09	2.25	6.38	1.15	**4.625**	**<0.001**
Macroinvertebrates	Abundance	4	180.60	1546	286.90	**-5.197**	**<0.001**
	TARISS	4	51.07	113	27.15	**-4.800**	**<0.001**
	Taxon Richness	1	7.11	19	3.72	**-4.974**	**<0.001**
	Chao-1	1	8.63	24	5.23	**-3.513**	**<0.001**

Spearman's correlation coefficients (R) between land-use class percentages (at different spatial scales) and water quality variables and macroinvertebrate indices are presented in Table S3 (Supplementary Information). Percentage Afromontane forest (dense forest) showed a positive correlation with dissolved oxygen, taxon richness, Chao-1 and TARISS score ($R > 0.3$, $p < 0.05$). Turbidity, ammonia, chlorophyll-a, phosphate and chemical oxygen demand were positively correlated with agricultural land (e.g., irrigated mixed crops) and barren land ($R > 0.3$, p= < 0.05), while negatively correlated with Afromontane forest ($R > -0.3$, $p=0.05$). Percentage irrigated mixed crops were negatively correlated with dissolved oxygen, taxon richness, Chao-1 and TARISS score ($R > -0.3$, $p=0.05$). Generally, the correlation coefficient between other land-use classes (at each spatial scale and for each spatial method of land-use estimation) and water quality variables was variable, similarly with macroinvertebrate indices.

The RDA results showed that variation in water quality was best explained by land-use at the watershed scale (dry season: R^2_{Adj} =0.71, p= 0.001, wet season: R^2_{Adj} =0.78, p= 0.001) as compared to other land-use estimators (see Table 2, Fig.4). Circular buffers around explained more variation in water quality (dry season: $0.28 \geq R^2_{Adj} \leq 0.68$, wet season: $0.31 \geq R^2_{Adj} \leq 0.61$) than circular buffers upstream each monitoring site (dry season: $0.26 \geq R^2_{Adj} \leq 0.65$, wet season: $0.35 \geq R^2_{Adj} \leq 0.54$). Most of the water quality variation was explained by the land-use at the largest spatial scale than at smaller spatial scales (for example, R^2_{Adj} = 0. 65 and R^2_{Adj} = 0. 54 for a 2000m circular buffer upstream the monitoring site in the dry and wet season respectively) (see Table 2). Macroinvertebrate assemblages could be best explained by a circular buffer upstream of the monitoring site at 2000m (dry season: R^2_{Adj} =0.11, wet season: R^2_{Adj} =0.24) compared to other spatial land-use estimators (see Table 2, Fig.4). Land-use of the watershed area upstream the monitoring site failed to explain any variation in macroinvertebrate assemblages (dry season: R^2_{Adj} = -0.009, wet season: R^2_{Adj} = -0.009). Overall, circular buffers upstream explained more variation in macroinvertebrate assemblages (dry: $0.05 \geq R^2_{Adj} \leq 0.11$, wet: $0.12 \geq R^2_{Adj} \leq 0.24$) than circular buffers around the monitoring sites (dry: $0.03 \geq R^2_{Adj} \leq 0.06$, wet: $0.08 \geq R^2_{Adj} \leq 0.19$). In the dry season, land-use at all scales (i.e., 100m to 2km) had similar effects on macroinvertebrate assemblages for circular buffers around the monitoring site (R^2_{Adj} = 0.03-0.06). For circular buffers upstream the monitoring site, land-use at 2km explained more variation in macroinvertebrate assemblages (dry: R^2_{Adj} =0.11, wet: R^2_{Adj} =0.24) compared to smaller spatial scales.

Table 2 Comparison of redundancy analysis (RDA) models showing the amount of variation in water quality variables and macroinvertebrate assemblages that can be explained using three different types of land-use estimators (i.e., circular buffer around the monitoring site, circular buffer upstream the monitoring site, and entire watershed area upstream the monitoring site) incorporating land-use at different spatial scales (i.e., 100m, 500m, 1km and 2km) in the dry wet seasons . Global F statistic and associated p value and coefficients of determination (R^2_{Adj}) are provided. Models are based on a forward selection procedure aimed to maximize the potential variation in water quality and macroinvertebrate assemblages that can be explained at each scale

Response Variable	**Buffer zone**	**Land use spatial scale**	**Dry Season**			**Wet Season**		
			R^2_{Adj}	**Global F**	**p Value**	**R^2_{Adj}**	**Global F**	**p Value**
(a) Water quality	Circular buffer around monitoring site	100m	0.28	8. 58	0.005**	0.31	7. 17	0.005**
		500m	0.30	18.07	0.001**	0.35	15.36	0.001**
		1km	0.51	15.32	0.001**	0.47	13.23	0.001**
		2km	0.68	23.54	0.001**	0.61	12.64	0.014*
	Circular buffer upstream the monitoring site	100m	0.26	7.73	0.001**	0.35	8.09	0.001**
		500m	0.36	22.23	0.001**	0.39	11.11	0.001**
		1km	0.37	11.07	0.001**	0.48	18.83	0.001**
		2km	0.65	12.89	0.001**	0.54	16.57	0.001**
	Entire watershed area upstream the monitoring site	watershed area	0.71	31.05	0.001**	0.78	8.17	0.001**
(b) Macro-invertebrates	Circular buffer around monitoring site	100m	0.03	2.54	0.008**	0.08	2.44	0.004**
		500m	0.01	2.25	0.004**	0.05	2.77	0.005**
		1km	0.02	2.89	0.007**	0.05	3.01	0.009**
		2km	0.06	3.08	0.001**	0.19	5.24	0.001**
	Circular buffer upstream the monitoring site	100m	0.05	2.82	0.009**	0.12	2.63	0.003**
		500m	0.06	2.94	0.011*	0.06	3.42	0.004**
		1km	0.07	3.52	0.002**	0.11	3.39	0.001**
		2km	0.11	3.03	0.006**	0.24	5.24	0.001**
	Entire watershed area upstream the monitoring site	watershed area	-0.002	*ns*	*ns*	-0.009	*ns*	*ns*

** = $p < 0.01$, * = $p < 0.05$

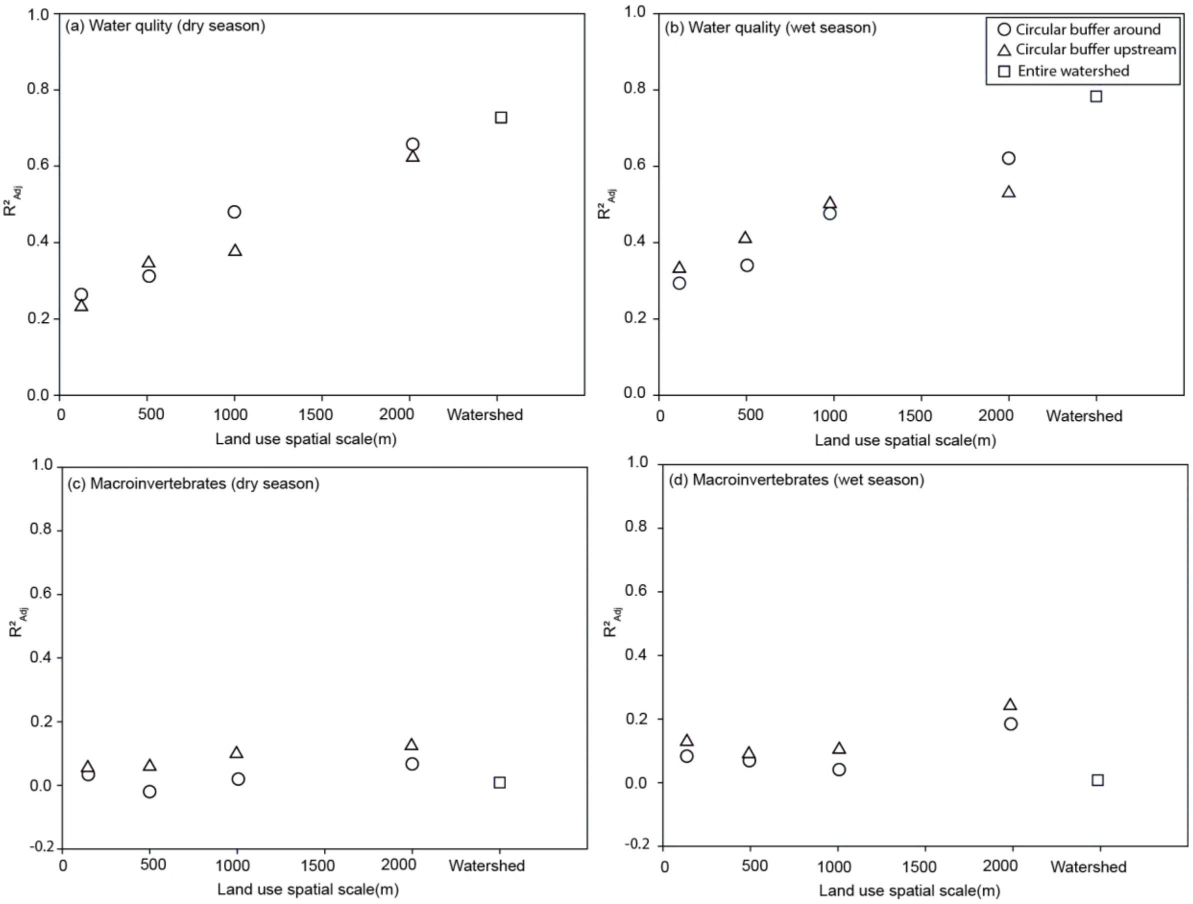

Fig. 4. Variation in physico-chemical water quality (a and b) and macroinvertebrate assemblages (c and d) explained by redundancy analysis models (R^2_{Adj}) based on three different types of land-use estimators (i.e., circle: circular buffer around the monitoring site, triangle: circular buffer upstream the monitoring site, and square: entire watershed area upstream the monitoring site) at different spatial scales (i.e., 100m, 500m, 1km and 2km) in the dry and wet seasons.

The effects of land-use spatial scale on TARISS score, taxon richness, and Chao-1) as determined by generalized linear models are presented in Table 3. AICs and R^2_{pseudo} values indicate that land-use best predicted variation in taxon richness when calculated for the entire watershed area above the monitoring sites (dry season: AIC = 137.49, R^2_{pseudo} = 0.20, wet season: AIC = 118.49, R^2_{pseudo} = 0.13), Fig. 5 and Fig. S1. When circular buffers were used, the best models were obtained when they were positioned around the monitoring sites (AIC = 171.29, R^2_{pseudo} = 0.18) and not upstream (AIC = 177.68, R^2_{pseudo} = 0.16) in the dry season, while there is no difference in the variation explained in the wet season (circular buffers around: AIC = 150.15, R^2_{pseudo} = 0.07, circular buffers upstream: AIC = 150.62, R^2_{pseudo} = 0.08). Similarly, land-use of the entire watershed area above the monitoring sites best predicted variation in TARISS scores (dry season: AIC= 254.46, R^2_{pseudo} = 0.54, wet season: AIC= 298.24, R^2_{pseudo} = 0.40). Best models are obtained when circular buffers are placed around the monitoring sites (AIC =383.38, R^2_{pseudo} = 0.37) and not positioned upstream (AIC=398.01, R^2_{pseudo} = 0.38) in the dry season, but this pattern was less clear in the wet season. Land-use best predicted variation in Chao-1 when calculated for the entire watershed area above the monitoring sites (dry season: AIC = 146.93, $R^2_{pseudo} = 0.37$, wet season: AIC = 135.82, $R^2_{pseudo} = 0.26$), Fig. 5 and Fig. S1. Circular buffers upstream and around the monitoring site explained almost similar variation in Chao-1 both in the dry ($181.78 \geq AIC \leq 202.06$, $0.14 \geq R^2_{pseudo} \leq 0.32$) and wet ($152.49 \geq AIC \leq 192.14$, $0.06 \geq R^2_{pseudo} \leq 0.19$) seasons. TARISS score formed good predictive models ($0.13 \geq R^2_{pseudo} \leq 0.54$) compared to taxon richness ($0.03 \geq R^2_{pseudo} \leq 0.20$), Chao-1($0.06 \geq R^2_{pseudo} \leq 0.37$), and macroinvertebrate abundances ($-0.006 \geq R^2_{Adj} \leq 0.24$).

Irrigated mixed crops, protected woodland and bushland, and sparse vegetation and bare land, were the land-use classes frequently retained in the forward selection procedure for the water quality RDA models (Table S4). Afromontane forest and sparse vegetation were the land-use classes often retained in the forward selection procedure for the macroinvertebrate RDA models. In the generalized linear models, Afromontane forest appeared to be the land-use class mostly retained in the backward and forward selection procedure, both for taxon richness, Chao-1 and TARISS score (Table S5).

Table 3 Comparison of the ability of generalized linear models to explain variation in macroinvertebrate biotic indices (i.e., TARISS, taxon richness, and Chao-1) using three different types of land-use estimators (i.e., circular buffer around the monitoring site, circular buffer upstream the monitoring site, and entire watershed upstream the monitoring site) incorporating land-use at different spatial scales (i.e., 100m, 500m, 1km and 2km) in the dry and wet season. Model performances are compared using the Akaike information criterion (AIC) and Mc Fadden's pseudo R^2 (the latter is a simple measure for model fit for generalized linear models). Models are based on backward and forward selection procedure aimed to maximize the potential variation in macroinvertebrate indices that can be explained at each spatial scale.

Response Variable	**Buffer zone**	**Land use spatial scale**	**Dry Season**		**Wet Season**	
			AIC	**McFadden's pseudo-R^2**	**AIC**	**McFadden's pseudo-R^2**
(a)TARISS	Circular buffer around the monitoring site	100m	457.02	0.28	529.68	0.13
		500m	383.38	0.37	419.83	0.33
		1km	396.29	0.39	442.5	0.31
		2km	280.21	0.17	408.59	0.38
	Circular buffer upstream the monitoring site	100m	491.11	0.22	523	0.15
		500m	398.01	0.38	421	0.34
		1km	461.22	0.27	400.26	0.36
		2km	457.02	0.29	408.67	0.37
	Entire watershed area upstream the monitoring site	watershed area	254.46	0.54	298.24	0.42
(b)Taxon richness	Circular buffer around the monitoring site	100m	179.55	0.15	153.63	0.04
		500m	175.66	0.17	152.10	0.07
		1km	171.29	0.18	150.15	0.07
		2km	180.21	0.17	152.49	0.10
	Circular buffer upstream the monitoring site	100m	184.66	0.10	153.81	0.03
		500m	177.68	0.16	150.93	0.03
		1km	182.5	0.10	151.29	0.11
		2km	195.1	0.14	150.62	0.08
	Entire watershed area upstream the monitoring site	watershed area	137.49	0.20	118.9	0.13
(c) Chao-1	Circular buffer around the monitoring site	100m	201.06	0.20	189.25	0.07
		500m	186.17	0.30	178.12	0.16
		1km	182.64	0.31	180.95	0.14
		2km	201.94	0.21	152.49	0.10
	Circular buffer upstream the monitoring site	100m	202.06	0.21	192.14	0.06
		500m	181.78	0.32	182.16	0.10
		1km	196.07	0.22	174.59	0.17
		2km	195.1	0.14	184.81	0.19
	Entire watershed area upstream the monitoring site	watershed area	146.93	0.37	135.82	0.26

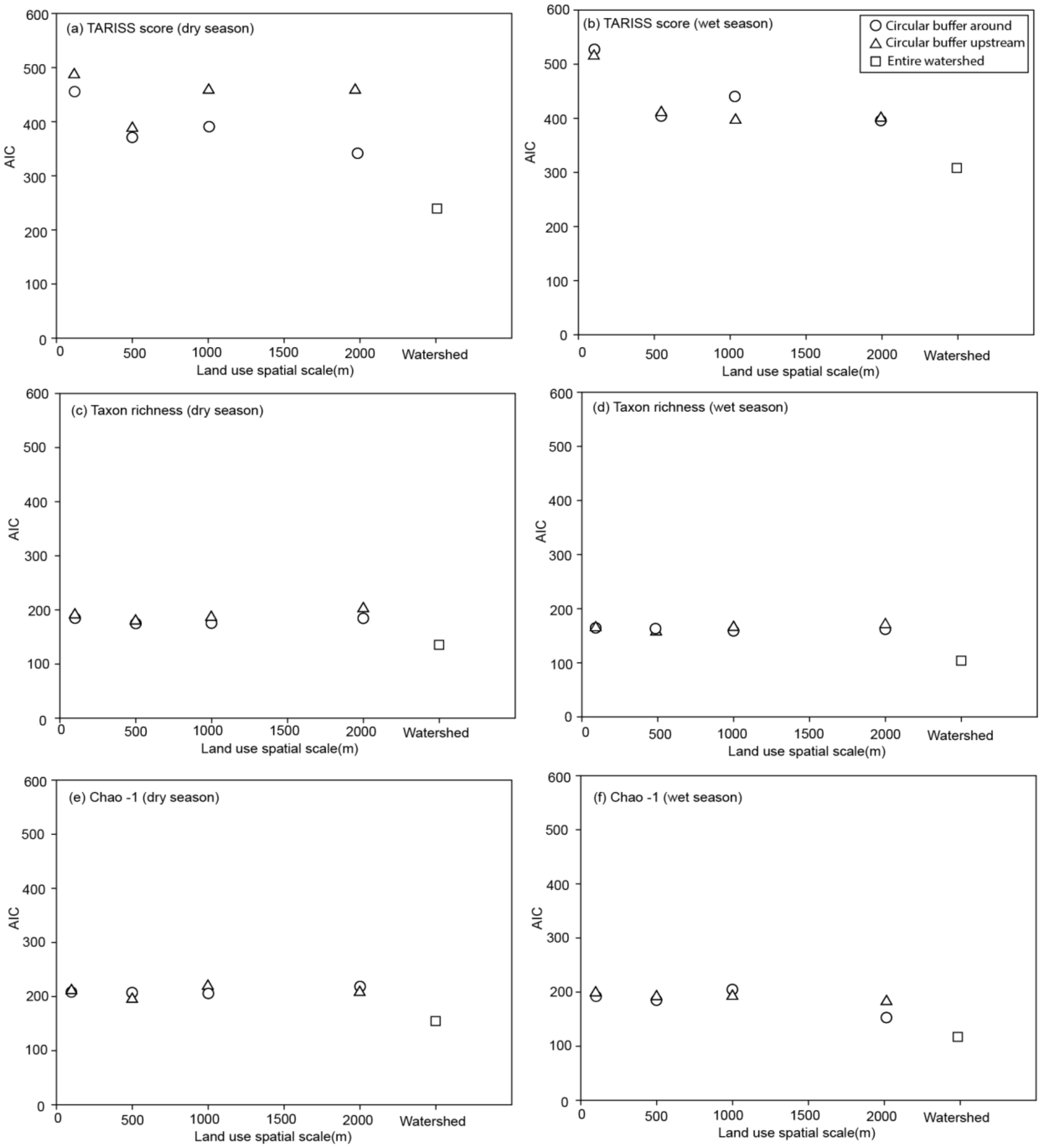

Fig. 5 Variation in TARISS score (a and b), taxon richness (c and d), and Chao-1 (e and f) explained by generalized linear models (AIC: lower AIC values indicate a better model) based on three different types of land-use estimators (circle: circular buffer around the monitoring site, triangle: circular buffer upstream the monitoring site, and square: entire watershed area upstream the monitoring site) at different spatial scales (i.e., 100m, 500m,1km and 2km) in the dry and wet seasons.

4. Discussion

We explored the performance of different spatial methods of land-use estimation that can be used to assess land-use activities at different spatial scales to predict river quality at a specific monitoring site. We found that the spatial estimate used, and the spatial scale considered can strongly confound the conclusions that can be drawn. We also discovered that physico-chemical water quality and macroinvertebrate assemblages responded differently to land-uses at different scales in the dry and wet seasons. However, the relationships were not always straightforward and clearly scale-dependent.

Nutrient concentrations and turbidity levels were closely related to land-use patterns, showing a positive correlation with percentage irrigated mixed crops and a negative correlation with percentage Afromontane forest. Agricultural land-use has been singled out as the main contributor of nutrient pollution in river systems worldwide (Ahearn et al., 2005; Bu et al., 2014; Tudesque et al., 2014; Nhiwatiwa et al., 2017). Several studies have also reported that intact riparian forests trap nutrients and sediments, and thereby inhibit their delivery to the stream (Richards and Host, 1994; Allan, 2004; Rolls et al., 2012; Bere et al., 2016). The observed variability in nutrient concentrations and turbidity levels between seasons, being generally high in the wet season, can be influenced by rainfall and subsequent runoff carrying sediment and nutrient loads from the catchment area to the river systems. These findings are in agreement with several studies in other regions (e.g., Kilonzo et al., 2014; Kalkhoff et al., 2016; Nhiwatiwa et al., 2017; Rostami et al., 2018) that demonstrated the increase of suspended solids and nutrient concentrations in river systems during rainfall events. We found positive correlations between macroinvertebrate biotic indices (i.e., taxon richness, Chao-1, and TARISS score) and forest cover and a negative correlation with agriculture land-use. These correlations are probably due to habitat alteration for stream macroinvertebrates by changes in land-use patterns, especially agriculture activities, as also suggested by Richards et al. (1996), Allan (2004), Li et al. (2012) and Magierowski et al. (2012) who reported similar patterns in different river systems.

Land-use of the entire watershed area upstream of the monitoring site better explained variation in physico-chemical water quality compared to other spatial methods of land-use estimation in the dry and wet seasons. These findings are consistent with similar studies in other regions. Ding et al. (2016) concluded that the entire watershed was better than the riparian or reach scale in explaining the overall water quality variation of low-order streams in the Dongjiang River basin, China. Tudesque et al. (2014) revealed that the strength of the relationship between water physical-chemistry and land-use patterns was strongest at the basin scale in the Adour-Garonne basin of South-Western France, emphasizing the importance of continuous processes of accumulation throughout the river gradient. Sponseller et al. (2001) also found that water chemistry was highly related to features of land-use at the watershed scale in the Roanoke River basin of southern Virginia. This shows that stream physico-chemical water quality conditions respond to cumulative anthropogenic, natural in-stream and/or allochthonous inputs

(Tudesque et al., 2014), in line with the linear concept of nutrient enrichment along the stream gradient, from the upper to the lower reaches (i.e., river continuum, Vannote et al., 1980). Pratt and Chang (2012) argue that including a larger land-use area is required in order to account for all and more distant sources of pollutants. In contrast, other studies have observed that water quality was more influenced by land-use at local scale. For example, Buck et al. (2004) found that nutrient and fecal coliform concentrations were better predicted by local riparian land-use rather than watershed land-use in small low-order streams in pasture catchments in New Zealand. They claimed that upstream land-use is more influential in larger streams, while local land-use may be more important in smaller streams. Likewise, Tran et al. (2010) found a stronger correlation between land-use and stream water quality at the 200-m buffer than when considering the watershed in the Champlain Lake Valley, New York State. These disparities in patterns are likely due to differences in study design (e.g., methods adopted to delineate the local buffer zone which produced different spatial data) that can lead to different hypotheses and more importantly different conclusions (Johnson et al., 2007; Ding et al., 2016). Disparities between studies can also be explained by differences in regional settings and water quality parameters of interest (Schiff and Benoit, 2007; Stanfield and Kilgour, 2012).

Land-use estimates from circular buffers around the monitoring sites explained more variation in physico-chemical water quality than when the areas were drawn immediately upstream. This pattern illustrates the importance of very localized drivers of water quality, with land-use in proximity to a monitoring site having more influence than similar activities further away. It is also possible that for pollution sources located at a greater distance upstream, landscape biogeochemical processes reset water quality parameters before the downstream river site is reached (Tran et al., 2010).

Surprisingly, even though upstream watershed land-use best predicted physico-chemical water quality, land-use evaluated at a smaller spatial scale (e.g., 100m) had stronger effects on benthic macroinvertebrate abundances. This suggests that the abundance of macroinvertebrate communities does not strongly respond to variation in the considered water quality variables. Instead, the detected effects of local land-use practices on biota are probably mediated by pollutants that were not measured such as pesticides and heavy metals. These strong local effects suggest that near-stream land-use can impact macroinvertebrate communities sufficiently to change the abundance, irrespective of land-use activities further upstream. Johnson et al. (2007) hypothesized that different organism groups may respond differently to different ecological scales, with benthic macroinvertebrates responding more to local scale (i.e., habitat-level) patterns and processes. Differences in scale of ecological effects may be related to the life history strategies of the individual organisms. For example, fish being mobile and long-lived may respond more to large scale factors, while sedentary macroinvertebrates may reveal higher responsiveness to local-scale factors (Dalu et al., 2017). Additionally, it is likely that localized input of pollutants (especially point sources of concentrated pollution such as flower farms), which might have a direct influence on macroinvertebrate assemblage might not have been captured in our sampling.

The observed local land-use effect on macroinvertebrate assemblages lends support to several previous studies. Richards and Host (1994) found significant effects of land-use on benthic macroinvertebrates at the local scale (100m buffer) and attributed this to alteration of stream habitats in watersheds of Lake Superior's North Shore in the USA. Sponseller et al. (2001) revealed that the relationship between land-use and macroinvertebrate assemblages was strongest at the local riparian buffer (200m sub-corridor scale) in the Roanoke River basin, southern Virginia. Similarly, Schiff and Benoit (2007) using redundancy analysis indicated that land-use within a 100-m riparian buffer had the largest effect on macroinvertebrate assemblages in the West River Watershed, USA. Sponseller et al. (2001) and Rios and Bailey (2006) suggested that macroinvertebrate abundances may be more sensitive to local land-use disturbances than ecosystem processes (incorporating both biotic and abiotic components) at broader spatial scales. However, a number of studies have shown the importance of watershed scale land-use factors in determining macroinvertebrate community compositions (Allan et al.,1997; Quinn et al., 1997; Young and Collier, 2009; Magierowski et al., 2012). Allan et al. (1997) indicated differences in land-use scales of investigation as the key factor leading to contrasting results. Magierowski et al. (2012) argue that the relative influence of local *versus* watershed scale will depend on the relative importance of the different environmental variables driving the macroinvertebrate communities, because these variables will respond differently to different scales of land-use. In addition, their relative importance in influencing community structure will vary among study sites.

The RDA results showed that the percentage variation in macroinvertebrate assemblages explained by land-use composition was not very large (i.e., < 25%). The unexplained variation was likely attributed to other important instream features influencing macroinvertebrates, such as substrate type (Beauger et al., 2006; Johnson et al., 2007; Weigel et al., 2003), water velocity (Statzner et al., 1988; Sandin and Johnson, 2004; Allan and Castillo, 2007; Li et al., 2012) or a set of multiple stressors (Dalu et al., 2017) which were not included in the models, plus sampling noise and other random factors.

Even though community structure (variation in abundance) seems to be controlled by local-scale processes, taxon richness and biotic indices (Chao-1 and TARISS) based on macroinvertebrates did respond to land-use at the scale of the watershed upstream of the monitoring sites. These results suggest that both abundance and biotic indices can yield complementary insights. Similarly, several other studies have shown that the land-use of the entire watershed upstream of the monitoring site was a better predictor of macroinvertebrate biotic indices than the land-use at the sampling site (Morley and Karr, 2002; Allan, 2004; Kuemmerlen et al., 2014; Tonkin et al., 2015). Weigel et al. (2003), for example, concluded that watershed-scale characteristics of streams of the Northern Lakes and Forest ecoregion, U.S.A, were more influential in defining macroinvertebrate assemblage attributes, whereas the reach-scale variables were more important in determining relative abundance and presence/absence. Our results and those of previous studies are consistent with the hierarchy theory which predicts that physical and biological variables at a small spatial scale are constrained by other variables at larger scales (Allen and Starr , 1982; Johnson et al., 2007). Such relationships are in line with Poff's (1997) hypothesis that species composition at a site is the product of environmental filters operating at successive spatial scales. Our results also indicated that the macroinvertebrate biotic index developed for Tanzania (i.e., TARISS) generated more reliable predictive models compared to Chao-1, taxon richness, and macroinvertebrate abundances, highlighting the usefulness of such indices as a basis for the assessment of the ecological condition of river systems.

Despite the potential of multi-spatial scale analyses to study the effects of land-use on river quality, they also present certain analytical challenges. Land-use percentages tend to be auto-correlated across spatial scales (Roth et al.,1996 and King et al., 2005). In our study system, autocorrelation of land-use practices occurred across scales, particularly in polygons with increasing radius. Land-use estimates at 100m and 500m were highly correlated and this was also to some extent the case for land-use in even larger polygons of 1km and 2km. In the case of very strong overlapping, it can be statistically impossible to distinguish which scale of land-use is most relevant for river quality. However, in this study, land-use at the watershed scale above the monitoring sites turned out to be largely independent of the other estimates. This illustrates that different land-use metrics can indeed yield largely the same, but sometimes also unique information. As such, we propose that multiscale studies always include exploratory analyses of autocorrelation among land-use variables at different spatial scales. Finally, it is noteworthy that studies of land-use effects on rivers exclusively focus on upstream conditions while the downstream condition can also affect the upstream situation. For instance, migration barriers such as downstream dams can preclude the presence of particular species. This is of particular relevance for fish and to a lesser extent for poorly dispersing invertebrates.

In conclusion, physico-chemical water quality and macroinvertebrate assemblages responded differently to land-use types at different spatial scales and may, therefore, be complementary and should be used simultaneously. Although these results were obtained for a specific study area, they illustrate well how the choice of spatial land-use metrics can bias conclusions of environmental impact studies in river systems. More importantly, our results illustrate a strong need for more studies to understand the influence of land-use activities on macroinvertebrate assemblages at multiple spatial scales, especially focusing on higher resolution land-use maps and sets of different landscape metrics. In addition to the generic insights that are relevant beyond the study system, it is noteworthy that to date, multi-scale relationships between land-use and river quality in the study region have not been assessed making this information of vital importance for sustainable management of water resources in the region.

References

Ahearn, D.S., Sheibley, R.W., Dahlgren, R.A., Anderson, M., Johnson, J., Tate, K.W., 2005. Land use and land cover influence on water quality in the last free-flowing river draining the western Sierra Nevada , California. J. Hydrol. 313, 234–247.

Akoto, O., Adiyiah, J., 2008. Dissolved nitrogen in drinking water resources of farming communities in Ghana. African J. Environ. Sci. Technol. 2, 31–35.

Al-badaii, F., Shuhaimi-othman, M., Gasim, M.B., 2013. Water Quality Assessment of the Semenyih River ,Selangor,Malaysia. J. Chem.

Allan, D.J., Castillo, M.M., 2007. Stream Ecology: Structure and Functioning of Running Waters, Second Edi. ed. Springer Netherlands.

Allan, D.J., Erickson, D.L., Fay, J., 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshw. Biol. 37, 149–161.

Allan, J.D., 2004. Landscapes and Riverscapes : The Influence of Land Use on Stream Ecosystems. Annu.Rev.Ecol.Syst 35, 257–84.

Allen, T.F.H., Starr, T.B., 1982. Hierarchy: Perspectives for ecological complexity, Chicago: University of Chicago Press. Chicago.

Al-shami, S.A., Rawi, C.S., Ahmad, A.H., Hamid, S.A., Nor, S.M., 2011. Influence of agricultural , industrial , and anthropogenic stresses on the distribution and diversity of macroinvertebrates in Juru River Basin ,Penang,Malaysia. Ecotoxicol. Environ. Saf. 74, 1195–1202.

Ambarita, M.N.D., Lock, K., Boets, P., Everaert, G., Hanh, T., Nguyen, T., Anne, M., Forio, E., Liz, P., Musonge, S., Suhareva, N., Bennetsen, E., Landuyt, D., Dominguez-granda, L., Goethals, P.L.M., 2016. Ecological water quality analysis of the Guayas river basin (Ecuador) based on macroinvertebrates indices. Limnologica 57.

Anderson, J.R., Hardy, E.E., Roach, J.T., Witmer, R.E., 1976. A land use and land cover classification system for use with remote sensor data:Geological Survey Professional Paper 964. Washington, United State of America.

APHA, 2012. Stand Methods for Examination of Water and Waste water, 22nd ed. ed. American Public Health Association,American Water Works Association,Water Environmental Federation, Washington, DC.

Asuero, A.G., Sayago, A., Gonzalez, A.G., 2006. The Correlation Coefficient : An Overview. Crit. Rev. Anal. Chem. 36, 41–59.

Azrina, M.Z., Yap, C.K., Ismail, A.R., Ismail, A., Tan, S.G., 2006. Anthropogenic impacts on the distribution and biodiversity of benthic macroinvertebrates and water quality of the Langat River , Peninsular Malaysia. Ecotoxicol. Environ. Saf. 64, 337–347.

Bagalwa, M., 2006. The impact of land use on water quality of the Lwiro River, Democratic Republic of Congo, Central Africa. African J. Aquat. Sci. 31, 137–143.

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid Bioassessment Protocols For Use in Streams and Wadeable RiversWadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish. Second Ed. EPA 841-B-99-002. U.S. Environ. Prot. Agency; Off. Water; Washington, DC, USA. Brewin.

Beauger, A., Lair, N., Marchan, R.P., Peiry, J.L., 2006. The distribution of macroinvertebrate assemblages in a reach of the River Allier (France), in relation to riverbed characteristics. Hydrobiologia 571, 63–76.

Beyene, A., Addis, T., Kifle, D., Legesse, W., Kloos, H., Triest, L., 2009. Comparative study of diatoms and macroinvertebrates as indicators of severe water pollution: Case study of the Kebena and Akaki rivers in Addis Ababa, Ethiopia. Ecol. Indic. 9, 381–392.

Brooks, A.J., Haeusler, T.I.M., Reinfelds, I., Williams, S., 2005. Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. Freshw. Biol. Biol. 50, 331–344.

Bu, H., Meng, W., Zhang, Y., Wan, J., 2014. Relationships between land use patterns and water quality in the Taizi River basin , China. Ecol. Indic. 41, 187–197.

Buck, O., Niyogi, D.K., Townsend, C.R., 2004. Scale-dependence of land use effects on water quality of streams in agricultural catchments. Environ. Pollut. 130, 287–299.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information, Theoretic Approach. Springer Science & Business Media.

Calijuri, M., Cunha, D., Queiroz, L., Moccellin, J., Miwa, A., 2008. Nutrients and chlorophyll- a concentrations in tropical rivers of Ribeira de Iguape Basin, SP, Brazil. Acta Limnol. Bras. 20, 131–138.

Chuman, T., Hruška, J., Oulehle, F., Gürtlerová, P., Majer, V., 2013. Does stream water chemistry reflect watershedcharacteristics? Environ. Monit. Assess. 185, 5683–5701.

Croft, P.S., 1986. A Key to the Major Groups of British Freshwater Invertebrates. Rep. Pub. FSC. 1986.

Dalu, T., Wasserman, R.J., Magoro, M.L., Mwedzi, T., Froneman, W.P., Weyl, O.L.F., 2017a. Variation partitioning of benthic diatom community matrices : Effects of multiple variables on benthic diatom communities in an Austral temperate river system. Sci. Total Environ. 601-602, 73–82.

Dalu, T., Wasserman, R.J., Tonkin, J.D., Alexander, M.E., Dalu, M.T.B., Motitsoe, S.N., Manungo, K.I., Bepe, O., Dube, T., 2017b. Assessing drivers of benthic macroinvertebrate community structure in African highland streams : An exploration using multivariate analysis. Sci. Total Environ. 601-602, 1340–1348.

Davies, B., Day, J., 1998. Vanishing Waters: Keys to common macroinvertebrate taxa of South African Inland Waters.

Diana, M., Allan, J.D., Infante, D., 2006. The Influence of Physical Habitat and Land Use on Stream Fish Assemblages in Southeastern Michigan. Am. Fish. Soc. Symp. 48, 359–374.

Dickens, C.W., Graham, P.M., 2002. The South African Scoring System (SASS) Version 5 Rapid Bioassessment Method for Rivers. African J. Aquat. Sci. 27, 1–10.

Ding, J., Jiang, Y., Liu, Q., Hou, Z., Liao, J., Fu, L., Peng, Q., 2016. Influences of the land use pattern on water quality in low-order streams of the Dongjiang River basin , China : A multi-scale analysis. Sci. Total Environ. 551-552, 205–216.

Dudgeon, D., 2010. Prospects for sustaining freshwater biodiversity in the 21st century : linking ecosystem structure and function. Curr. Opin. Environ. Sustain. 2, 422–430.

Elisante, E., Muzuka, A.N.N., 2016. Assessment of sources and transformation of nitrate in groundwater on the slopes of Mount Meru , Tanzania. Environ. Earth Sci. 75, 1–15.

Gerber, A., Gabriel, M.J.M., 2002. Aquatic Invertebrates of South African Rivers: Field Guide. Institute for Water Quality Studies.

Harding, J.S., Young, R.G., Hayes, J.W., Shearer, K.A., Stark, J.D., 1999. Changes in Agricultural Intensity and River Health Along a River Continuum. Freshw. Biol. 42, 345–357.

Hemp, A., 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. Glob. Chang. Biol. 11, 1013–1023.

Hering, D., Johnson, R.K., Kramm, S., Schmutz, S., Szoszkiewicz, K., Verdonschot, P.F.M., 2006. Assessment of European streams with diatoms , macrophytes , macroinvertebrates and fish : a comparative metric-based analysis of organism response to stress. Freshw. Biol. 51, 1757–1785.

Hrodey, P.J., Sutton, T.M., Frimpong, E.A., 2009. Land-Use Impacts on Watershed Health and Integrity in Indiana Warmwater Streams. Am. Midl. Nat. 16, 76–95.

Johnson, R.K., Furse, M.T., Hering, D., Sandin, L., 2007. Ecological relationships between stream communities and spatial scale : implications for designing catchment- level monitoring programmes. Freshw. Biol. 52, 939–958.

Kaaya, L.T., Day, J.A., Dallas, H.F., 2015. Tanzania River Scoring System (TARISS): a macroinvertebrate-based biotic index for rapid bioassessment of rivers. African J. Aquat. Sci. 40, 109–117.

Kalkhoff, S.J., Hubbard, L.E., Tomer, M.D., James, D.E., 2016. Effect of variable annual precipitation and nutrient input on nitrogen and phosphorus transport from two Midwestern agricultural watersheds. Sci. Total Environ. 559, 53–62.

Kang, J., Lee, W.S., Cho, H.K., Ki, J.S., Cha, M.S., Kim, H.J., 2010. Linking land-use type and stream water quality using spatial data of fecal indicator bacteria and heavy metals in the Yeongsan river basin. Water Res. 44, 4143–4157.

King, R.S., Baker, M.E., Whigham, D.F., Weller, D.E., Jordan, T.E., Kazyak, P.F., Hurd, M.K., 2005. Spatial Considerations for Linking Watershed Land Cover to Ecological Indicators in Streams. Ecol. Appl. 15, 137–153.

Kiptala, J.K., Mohamed, Y., Mul, M.L., Cheema, M.J.M., Van Der Zaag, P., 2013. Land use and land cover classification using phenological variability from MODIS vegetation in the Upper Pangani River Basin , Eastern Africa. Phys. Chem. Earth 66, 112–122.

Kiptala, J.K., Mul, M.L., Mohamed, Y., Zaag, P. van der, 2013. Modelling stream flow and quantifying blue water using modified STREAM model in the Upper Pangani River Basin , Eastern Africa. Hydrol. Earth Syst. Sci. 10, 15771–15809.

Klein, I., Gessner, U., Kuenzer, C., 2012. Regional land cover mapping and change detection in Central Asia using MODIS time-series. Appl. Geogr. 35, 219–234.

Kuemmerlen, M., Schmalz, B., Guse, B., Cai, Q., Fohrer, N., Jähnig, S.C., 2014. Integrating catchment properties in small scale species distribution models of stream macroinvertebrates. Ecol. Modell. 277, 77–86.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Legendre, P., Lengendre, L., 2012. Numerical Ecology. 2nd English Edition. Elsevier Science, Amsterdam, Netherlands.

Legendre, P., Oksanen, J., Braak, C.J.F., 2011. Testing the significance of canonical axes in redundancy analysis. Methods Ecol. Evol. 269–277.

Li, F., Chung, N., Bae, M., Kwon, Y., Park, Y., 2012. Relationships between stream macroinvertebrates and environmental variables at multiple spatial scales. Freshw. Biol. 57, 2107–2124. h

Lumbreras, A., Marques, J.T., Belo, A.. ., Cristo, M., Fernandes, M., Galioto, D., Machado, M., Mira, A., Sá-Sousa, P., Silva, R., Sousa, L.., Pinto-Cruz, C., 2016. Assessing the conservation status of Mediterranean temporary ponds using biodiversity : a new tool for practitioners. Hydrobiologia 782, 187–199.

Magierowski, R.H., Davies, P.E., Read, S.M., Horrigan, N., 2012. Impacts of land use on the structure of river macroinvertebrate communities across Tasmania , Australia : spatial scales and thresholds. Mar. Freshw. Res. 63, 762–776.

Mbonile, M.J., 2005. Migration and intensification of water conflicts in the Pangani Basin , Tanzania. Habitat Int. 29, 41–67.

Meador, M. rR, Goldstein, R.M., 2003. Assessing Water Quality at Large Geographic Scales : Relations Among Land Use , Water Physicochemistry , Riparian Condition , and Fish Community Structure. Environ. Manage. 31, 504–517.

Meru District Council, 2013. Meru district council profile. Arusha, Tanzania. p80 (unpublished report).

Morley, S.A., Karr, J.R., 2002. Assessing and Restoring the Health of Urban Streams in the Puget Sound Basin. Conserv. Biol. 16, 1498–1509.

Mouri, G., Takizawa, S., Oki, T., 2011. Spatial and temporal variation in nutrient parameters in stream water in a rural-urban catchment, Shikoku, Japan: Effects of land cover and human impact. J. Environ. Manage. 92, 1837–1848.

National Sample Census of Agriculture(NSCA), 2007. United Republic of Tanzania, Regional Report: Arusha Region: Volume Vb.

Nhiwatiwa, T., Dalu, T., Brendonck, L., 2017a. Impact of irrigation based sugarcane cultivation on the Chiredzi and Runde Rivers quality, Zimbabwe.

Nhiwatiwa, T., Dalu, T., Sithole, T., 2017b. Assessment of river quality in a subtropical Austral river system : a combined approach using benthic diatoms and macroinvertebrates. Appl. Water Sci. 7, 4785–4792.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, H.M.H., Szoecs, E., Wagner, H., 2016. Vegan Community Ecology Package version 2.4-1.

PBWO/IUCN, 2007a. IUCN Water and Nature Initiative and Pangani Basin Water Board. River Health Assessment Final Report, Pangani River Basin Flow Assessment. Moshi, Tanzania.

PBWO/IUCN, 2007b. Pangani River System: State of the Basin Report 2007.Moshi,Tanzania.

Poff, N.L., 1997. Stream Ecology Landscape filters and species traits : towards mechanistic understanding and prediction in stream ecology. J. North Am. Benthol. Soc. 16, 391–409.

Pratt, B., Chang, H., 2012. Effects of land cover , topography , and built structure on seasonal water quality at multiple spatial scales. J. Hazard. Mater. 209-210, 48–58.

Quinn, J.M., Cooper, A.B., Colley, R.J.D., Rutherford, J.C., Williamson, R.B., 1997. Land use effects on habitat , water quality , periphyton , and benthic invertebrates in Waikato , New Zealand , hill-country streams. New Zeal. J. Mar. Freshw. Res. 31, 579–597.

Richards, C., Haro, R.J., Johnson, L.B., Host, G.E., 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. Biol. 37, 219–230.

Richards, C., Host, G., 1994. Examining Land Use Influences on Stream Habitats and Macroinvertebrates: A Gis Approach. Am. Water Resour. Assoc. 30, 729–738.

Richards, C., Johnson, L.B., Host, G.E., 1996. Landscape-scale influences on stream habitats and biota. Can. J. Fish. Aquat. Sci. 53, 295–311.

Rimer, A.E., Nissen, J.A., Reynolds, D.E., 1978. Characterization and impact of stormwater runoff from various land cover types. Water Pollut. Control Fed. 50, 252–264.

Rios, S.L., Bailey, R.C., 2006. Relationship between riparian vegetation and stream benthic communities at three spatial scales. Hydrobiologia 553, 153–160.

Rosenberg, D.M.., Resh, V.H., 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. Ecology 75, 267–268.

Rostami, S., He, J., Hassan, Q.K., 2018. Riverine Water Quality Response to Precipitation and Its Change. Environments 5, 1–17.

Roth, N.E., Allan, J.D., Erickson, D.L., 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landsc. Ecol. 11, 141–156.

Schiff, R., Benoit, G., 2007. Effects Of Impervious Cover At Multiple Spatial Scales On Coastal Watershed Streams. J. Am. Water Resour. Assoc. 43, 712–730.

Selemani, J.R., Zhang, J., Muzuka, A.N.N., Njau, K.N., Zhang, G., Mzuza, M.K., Maggid, A., 2017. Nutrients' distribution and their impact on Pangani River Basin's ecosystem – Tanzania. Environ. Technol. 702–716.

Shen, Z., Hou, X., Li, W., Aini, G., Chen, L., Gong, Y., 2015. Impact of landscape pattern at multiple spatial scales on water quality : A case study in a typical urbanised watershed in China. Ecol. Indic. 48, 417–427.

Shi, P., Zhang, Y., Li, Z., Li, P., Xu, G., 2016. Influence of land use and land cover patterns on seasonal water quality at multi saptial scales. Catena 151, 182–190. h

Siddig, A.A.H., Ellison, A.M., Ochs, A., Villar-leeman, C., Lau, M.K., 2016. How do ecologists select and use indicator species to monitor ecological change ? Insights from 14 years of publication in Ecological Indicators. Ecol. Indic. 60, 223–230.

Sliva, L., Williams, D.D., 2001. Buffer zone versus whole catchment approaches to studying land use impact on river water quality. Water Res. 35, 3462–72.

Sliva, L., Williams, D.D., 2001. Buffer Zone Versus Whole Catchment Approaches To Studying Land Use Impact On River Water Quality. Watater Res. 35, 3462–3472.

Sponseller, R.A., Benfield, E.F., Valeth, H.M., 2001. Relationships between land use , spatial scale and stream macroinvertebrate communities. Freshw. Biol. 46, 1409–1424.

Stanfield, L.W., Kilgour, B.W., 2012. How Proximity Of Land Use Affects Stream Fish And Habitat. River Res. Appl. 1–15. h

Statzner, B., Gore, J.A., Resh, V.H., 1988. Hydraulic Stream Ecology : Observed Patterns and Potential Applications Hydraulic stream. J. North Am. Benthol. Soc. 7, 307–360.

Taylor, R., 1990. Interpretation of the Correlation Coefficient A Basic Review. J. Diagnostic Med. Sonogr. 6, 35–39.

Tonkin, J.D., Shah, D.N., Kuemmerlen, M., Li, F., Cai, Q., Haase, P., Jähnig, S.C., 2015. Climatic and Catchment-Scale Predictors of Chinese Stream Insect Richness Differ between Taxonomic Groups. PLoS One 10, 1–17.

Townsend, C.R., Doledec, S., Norris, R., Peacock, K., Arbuckle, C., 2003. The influence of scale and geography on relationships between stream community composition and landscape variables : description and prediction. Freshw. Biol. 48, 768–785.

Tran, C.P., Bode, R.W., Smith, A.J., Kleppel, G.S., 2010. Land-use proximity as a basis for assessing stream water quality in New York State (USA). Ecol. Indic. 10, 727–733.

Tudesque, L., Tisseuil, C., Lek, S., 2014. Scale-dependent effects of land cover on water physico-chemistry and diatom-based metrics in a major river system , the Adour-Garonne basin (South Western France). Sci. Total Environ. 466-467, 47–55.

Vannote, R.L., Minshall, G.W., Cummins, K., Sedell, J.R., 1980. The River Continuum Concept. Can J Fish Aquat Sci 37, 130–7.

Wang, L., Lyons, J., Rasmussen, P., Seelbach, P., Simon, T., Wiley, M., Kanehl, P., Baker, E., Niemela, S., Stewart, P.M., 2003. Watershed , reach , and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion , U.S .A. Can. J. Fish. Aquat. Sci 60, 491–505.

Weigel, B.M., Wang, L., Rasmussen, P.W., Butcher, J.T., Stewart, P.M., Simon, T.P., Wiley, M.J., 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the Northern Lakes. Freshw. Biol. 48, 1440–1461.

Wilcoxon, F., 1945. Individual Comparisons by Ranking Methods. Biometrics Bull. 1, 80–83.

Wilson, C., Weng, Q., 2010. Assessing Surface Water Quality and Its Relation with Urban Land Cover Changes in the Lake Calumet Area, Greater Chicago. Environ. Manage. 45, 1096–1111.

Young, R.G., Collier, K.., 2009. Contrasting responses to catchment modification among a range of functional and structural indicators of river ecosystem health. Freshw. Biol. 54, 2155–2170.

Zuur, A.K., Ieno, E.N., Smith, G.M., 2007. Analysing Ecological Data. Springer + Business Media,LLC,Sring Street, New York,NY 10013,USA.

Supplementary Information to Chapter 2

Table S1 Description of eighteen land-use classes in the Usa-Kikuletwa River Catchment

Land use class	**Description**
Afromontane Forest	Land with natural tree canopy cover of more than 10 percent
Water Bodies	Permanent water body such as rivers and lakes
Wetland and Swamps	Natural area covered with water and aquatic vegetation
Irrigated Banana and coffee	Irrigated areas (rain-fed during rainy season) dominated with mixer of banana and coffee on the same farm plot
Irrigated Banana, Coffee and Maize	Irrigated areas (rain-fed during rainy season) dominated by mixer of crops such as banana, coffee and maize on the same farm plot
Irrigated mixed crops	Irrigated areas dominated by irrigated vegetables such as tomatoes, onions, eggplant, and irrigated cash crops such maize and rice
Irrigated sugarcane	Irrigated and supplement rain-fed areas used for production of sugarcane
Protected woodland	Natural tree covered areas with few grasses legally protected
Grazed woodland	Tree covered areas with few grasses which occurred naturally and used for grazing from month of June to December
Grazed Shrub land	Areas used for grazing, having plant community dominated with grasses, shrubs and small trees
Grazed grassland	Areas with natural grassland used mainly for grazing
Urban and/or Settlement	Includes residential area, commercial area, and industrial area
Sparse vegetation and Bare land	Areas with scattered short vegetation which grow naturally covering about 5-15% of the land (Klein et al., 2012)
Sparse vegetation and/or bare land	Areas with scattered vegetation mixed with bare land (Klein et al., 2012)
Shrub land and Thickets	Area with plant community characterized by vegetation dominated with shrubs (about 50%) and more with trees close together
Afro alpine forest	Shrub lands and grasslands containing plants found at lower altitudes, in middle and high latitudes.
Subalpine grassland	Areas in high altitude below the tree zone dominated by *Helichrysum* cushion vegetation (Hemp, 2005)
Subalpine bushland	Areas in high altitude below the tree zone dominated by *Erica* vegetation (Hemp, 2005)

Table S2 Spearman correlation coefficient (R) of land-use classes among spatial scales (i.e. 100m, 500m, 1km, and 2km) in the three different land-use estimators (i.e. circular buffer around the monitoring site, circular buffer upstream the monitoring site, and entire watershed upstream the monitoring site). Values in bold are significant correlations at $p < 0.05$.

Spatial method of land use estimation	**Percentage Land use**	**Reference**	**% Mean± SE**	**Spearman R**			
				500m	**1km**	**2km**	**Watershed**
(a) Circular buffer around the monitoring site	Afromontane Forest	100m	17.2 ± 4.15	**0.79**	**0.7**	**0.73**	0.04
		500m	7 .51± 2.66		**0.97**	**0.91**	-0.1
		1km	5.99 ± 2.25			**0.95**	-0.18
		2km	6.41 ± 2.14				-0.21
	Barren Land	100m	0.46±0.28	0.33	0.28	0.1	0.16
		500m	1.79±0.47		**0.82**	**0.69**	**0.77**
		1km	1.97±0.46			**0.84**	**0.62**
		2km	2.23±0.54				**0.69**
	Grazed Shrub Land	100m	0.06±0.06	**0.58**	0.28	0.27	0.15
		500m	0.27±0.07		**0.75**	**0.63**	0.23
		1km	0.36±0.06			**0.76**	0.14
		2km	0.43±0.06				**0.41**
	Grazed Woodland	100m	1.26±0.44	**0.7**	**0.62**	**0.48**	-0.04
		500m	0.47±0.12		**0.89**	**0.67**	-0.1
		1km	0.40±0.07			**0.84**	-0.04
		2km	0.44±0.05				0.23
	Protected Woodland/Bush	100m	2.19±0.74	**0.62**	**0.62**	**0.59**	0.19
		500m	1.98±0.44		**0.93**	**0.88**	0.36
		1km	2.37±0.58			**0.98**	0.38
		2km	2.94±0.75				0.39
	Irrigated Mixed Crops	100m	27.1±3.99	**0.8**	**0.78**	**0.67**	**0.55**
		500m	28.45±2.76		**0.94**	**0.86**	**0.51**
		1km	24.68±2.64			**0.95**	**0.59**
		2km	27.4±2.22				0.6
	Irrigated Banana and Coffee	100m	28.76±3.46	**0.88**	**0.84**	**0.83**	**-0.41**
		500m	29.87±4.02		**0.97**	**0.93**	**-0.55**
		1km	29.40±4.07			**0.97**	**-0.59**
		2km	28.07±3.75				**-0.59**
	Irrigated Banana, Coffee and Maize	100m	15.54±2.59	**0.52**	**0.48**	**0.41**	0.22
		500m	17.65±2.10		**0.94**	**0.85**	0.19
		1km	18.24±2.12			**0.93**	0.13
		2km	18.07±2.01				0.18
	Wetland	100m	0.06±0.06	0.01	-0.02	-0.03	-0.06
		500m	0.27±0.09		**0.92**	**0.69**	-0.004
		1km	0.22±0.05			**0.85**	0.04

		2km	0.28±0.05				0.17
	Sparse Vegetation or Bare land	100m	1.86±0.63	**0.57**	**0.42**	**0.33**	0.03
		500m	3.70±0.75		**0.9**	**0.77**	0.19
		1km	4.56±0.74			**0.83**	0.14
		2km	4.54±0.57				0.25
	Shrub and Thickest	100m	5.31±1.46	**0.75**	**0.57**	**0.38**	**0.43**
		500m	7.36±1.22		**0.9**	**0.79**	**0.66**
		1km	7.59±1.09			**0.94**	**0.63**
		2km	8.57±1.31				**0.59**
	Water Bodies	500m	0.01±0.01		**0.99**	0.21	-0.07
		1km	0.003±0.002			0.21	-0.07
		2km	0.11±0.09				-0.06
	Grazed Grassland	500m	0.03±0.01		**0.61**	**0.49**	0.16
		1km	0.05±0.03			**0.98**	**0.44**
		2km	0.15±0.10				**0.43**
	Sparse Vegetation	500m	0.01±0.007		0.24	0.13	-0.07
		1km	0.02±0.01			**0.72**	0.13
		2km	0.03±0.01				**0.72**
	Irrigated Maize	500m	0.05±0.02		**0.84**	**0.62**	**0.43**
		1km	0.04±0.01			**0.88**	0.24
		2km	0.05±0.008				0.14
	Afro alpine Forest	500m	0.059±0.05		**1**	**0.99**	**-0.66**
		1km	0.014±0.01			**0.99**	-0.06
		2km	0.003±0.003				-0.06
	Urban or Building	500m	0.01±0.008		**0.81**	-0.02	-0.1
		1km	0.02±0.007			-0.04	-0.1
		2km	0.21±0.18				0.06
	Subalpine Forest	1km	0.002±0.001			**0.95**	-0.07
		2km	0.001±0.0005				-0.08
(b) Circular buffer upstream the monitoring site	Afromontane Forest	100m	14.44±3.86	**0.84**	**0.83**	**0.74**	-0.02
		500m	7.89±3.18		**0.93**	**0.8**	-0.15
		1km	10.23±3.47			**0.94**	-0.18
		2km	14.23±3.96				-0.22
	Barren Land	100m	1.03±0.84	**0.55**	0.26	0.38	**0.78**
		500m	1.74±0.49		**0.69**	**0.57**	**0.7**
		1km	1.67±0.46			**0.9**	**0.66**
		2km	2.07±0.61				**0.78**
	Grazed Woodland	100m	0.93±0.33	**0.68**	**0.44**	-0.009	-0.15
		500m	0.48±0.09		**0.81**	0.2	0.04
		1km	0.36±0.05			0.3	0.2
		2km	0.44±0.13				**0.5**
	Protected Woodland/Bush	100m	1.09±0.51	**0.44**	**0.72**	**0.58**	**0.4**
		500m	1.86±0.40		**0.87**	**0.65**	0.27

		1km	1.87±0.42			**0.82**	**0.44**
		2km	1.78±0.44				**0.5**
	Irrigated Mixed Crops	100m	25.03±3.76	**0.81**	**0.79**	**0.61**	**0.57**
		500m	26.20±2.88		**0.94**	**0.82**	**0.5**
		1km	24.27±2.67			**0.87**	**0.65**
		2km	18.93±2.21				**0.57**
	Irrigated Banana and Coffee	100m	35.49±3.86	**0.77**	**0.79**	**0.68**	-0.28
		500m	30.97±4.24		**0.94**	**0.68**	**-0.47**
		1km	30.35±4.08			**0.86**	**-0.45**
		2km	32.75±4.10				-0.3
	Irrigated Banana, Coffee and Maize	100m	15.31±2.35	**0.55**	**0.67**	**0.72**	0.17
		500m	20.50±2.71		**0.93**	**0.68**	0.14
		1km	20.83±2.56			**0.82**	0.18
		2km	18.17±2.22				**0.42**
	Wetland	100m	0.06±0.06	0.02	-0.05	-0.03	0.06
		500m	0.08±0.03		**0.61**	-0.05	-0.02
		1km	0.09±0.03			-0.04	0.23
		2km	0.67±0.56				**0.41**
	Sparse Vegetation or Bare land	100m	0.88±0.32	0.36	**0.46**	0.17	0.17
		500m	3.13±0.71		**0.93**	**0.42**	0.17
		1km	2.99±0.63			**0.47**	0.15
		2km	3.03±0.48				**0.54**
	Shrub and Thickest	100m	5.70±1.22	**0.79**	**0.72**	**0.53**	**0.46**
		500m	6.71±1.19		**0.84**	**0.73**	**0.66**
		1km	5.90±1.09			**0.81**	**0.64**
		2km	6.86±1.35				**0.71**
	Grazed Shrub Land	500m	0.27±0.09		**0.75**	**0.49**	0.1
		1km	0.30±0.08			**0.68**	0.08
		2km	0.24±0.04				**0.46**
	Grazed Grassland	500m	0.03±0.03		**0.99**	**0.99**	**0.46**
		1km	0.11±0.11			**0.99**	**0.41**
		2km	0.12±0.11				**0.42**
	Sparse Vegetation	500m	0.005±0.005		**0.46**	-0.01	-0.04
		1km	0.004±0.002			-0.01	0.08
		2km	0.02±0.02				**0.95**
	Irrigated Maize	500m	0.007±0.004		0.11	0.17	-0.07
		1km	0.03±0.01			**0.6**	0.32
		2km	0.03±0.007				0.14
	Subalpine Forest	500m	0.02±0.02		0.05	-0.002	-0.04
		1km	0.001±0.0			**0.61**	-0.05
		2km	0.001±0.0				-0.09
	Urban or Building	500m	0.002±0.002		0.33	0.13	-0.06

		1km	0.007±0.003			**0.4**	-0.14
		2km	0.007±0.002				0.33
	Water Bodies	1km	0.002±0.001			0.22	0.32
		2km	0.004±0.001				**0.51**
	Afro alpine Forest	2km	0.005±0.003				-0.09

Table S3 Spearman correlation coefficient (R) between land-use classes and water quality variables and macroinvertebrate indices among spatial scales (i.e., 100m, 500m, 1km, and 2km) in the three different land-use estimators (i.e., circular buffer around the monitoring site, circular buffer upstream the monitoring site, and entire watershed upstream the monitoring site). Values in bold are significant correlations at $p < 0.05$. GSL=Grazed Shrubland, GGL=Grazed Grassland, BAL=Barren Land, SPV=Sparse Vegetation, IRM=Irrigated Maize, AAF=Afro Alpine Forest, SAF=Subalpine Forest, GRZ=Grazed Woodland, PWB=Protected Woodland/Bushland, IMC=Irrigated Mixed Crops, IBC=Irrigated Banana and Coffee, IBCM=Irrigated Banana, Coffee and Maize, WTL=Wetland, UB=Urban Buildings, SVB=Sparse Vegetation or Bare land, SRT=Shrub land or/ and Thickets, WR=Water Bodies, AF=Afromontane Forest.

Spatial method of land use estimation	**Spatial scale**	**Response Variable**	**Land use class**								
			GS L	**GG L**	**BA L**	**SP**	**IR**	**AA**	**SA**	**GRZ**	**PWB**
(a)Circular buffer around the monitoring site	100m	pH	0.03		0.24					**0.31**	**0.37**
		EC (µC/cm)	0.12		-0.03					**0.37**	**0.50**
		DO (mg/L)	0.02		0.01					-0.29	**-0.42**
		Turb (ftu)	0.19		0.26					0.22	**0.35**
		FL (mg/L)	0.14		0.03					0.24	**0.32**
		NH$_3$-N (mg/L)	0.25		0.29					0.18	**0.42**
		NO$_3$--N (mg/L)	0.21		0.13					0.15	0.28
		PO$_4^{3-}$ (mg/L)	0.15		0.17					0.25	**0.41**
		Chl_a (mg/L)	0.21		0.14					0.10	**0.33**
		TN (mg/L)	-0.14		-0.10					-0.06	-0.01
		COD (mg/L)	0.17		0.15					0.18	**0.41**
		TP (mg/L)	0.19		0.12					0.20	**0.22**
		TARISS		0.02	-0.10					-0.22	-0.15
		Taxon_R		-0.07	-0.17					-0.15	-0.09
	500m	pH	**0.53**	0.24	**0.73**	0.04	0.03	0.24		**0.43**	**0.55**
		EC (µC/cm)	**0.36**	**0.33**	**0.54**	0.23	-0.09	0.26		0.26	**0.53**
		DO (mg/L)	-0.25	-0.10	-0.45	-0.17	0.05	-0.15		-0.19	**-0.35**
		Turb (ftu)	**0.70**	0.16	**0.77**	0.13	0.08	-0.09		**0.42**	**0.50**
		FL (mg/L)	0.21	0.24	**0.43**	0.12	-0.03	0.25		0.11	**0.35**
		NH$_3$-N (mg/L)	**0.68**	**0.33**	**0.81**	0.11	-0.09	0.14		**0.31**	**0.60**
		NO$_3$--N (mg/L)	**0.32**	**0.37**	**0.45**	0.23	0.16	0.17		0.11	**0.43**
		PO$_4^{3-}$ (mg/L)	**0.45**	**0.41**	**0.73**	0.20	0.01	0.24		0.29	**0.57**
		Chl_a (mg/L)	**0.52**	0.24	**0.71**	-0.06	-0.10	0.17		0.21	**0.43**
		TN (mg/L)	-0.12	-0.12	-0.05	0.04	-0.18	-0.17		0.15	0.17
		COD (mg/L)	**0.48**	**0.34**	**0.68**	0.08	-0.03	0.26		0.14	**0.52**
		TP (mg/L)	**0.45**	0.24	**0.58**	0.17	0.02	0.14		**0.36**	**0.50**
		TARISS	-0.17	0.23	-0.14	-0.01	-0.26	0.18		-0.22	-0.02
		Taxon_R	-0.29	0.09	-0.18	0.17	-0.24	0.05		-0.17	-0.04
	1km	pH	**0.62**	**0.32**	**0.73**	0.22	0.06	0.24	**-0.34**	**0.46**	**0.59**
		EC (µC/cm)	**0.47**	**0.41**	**0.48**	0.27	-0.10	0.26	**-0.37**	**0.33**	**0.59**
		DO (mg/L)	-0.20	-0.14	**-0.34**	-0.13	0.00	-0.15	0.00	-0.19	**-0.34**
		Turb (ftu)	**0.70**	**0.37**	**0.81**	0.23	0.11	-0.09	**-0.37**	**0.35**	**0.51**
		FL (mg/L)	**0.31**	**0.39**	**0.33**	0.20	-0.04	0.25	-0.29	0.14	**0.41**
		NH$_3$-N (mg/L)	**0.72**	**0.51**	**0.80**	**0.30**	-0.11	0.14	**-0.30**	**0.32**	**0.59**
		NO$_3$--N (mg/L)	**0.40**	**0.49**	**0.38**	**0.35**	0.13	0.17	-0.18	0.17	**0.42**
		PO$_4^{3-}$ (mg/L)	**0.63**	**0.52**	**0.71**	**0.36**	0.01	0.24	**-0.44**	**0.36**	**0.62**
		Chl_a (mg/L)	**0.49**	**0.37**	**0.67**	0.17	-0.22	0.17	0.14	0.17	**0.44**
		TN (mg/L)	-0.06	**-0.33**	0.01	-0.22	-0.29	-0.17	0.25	0.14	0.13
		COD (mg/L)	**0.47**	**0.49**	**0.60**	0.25	0.03	0.26	**-0.36**	0.16	**0.51**
		TP (mg/L)	**0.52**	**0.34**	**0.60**	0.16	-0.20	0.14	-0.17	**0.36**	**0.52**
		TARISS	-0.17	-0.07	-0.14	-0.15	**-0.39**	0.18		-0.03	-0.01
		Taxon_R	-0.26	-0.13	-0.21	-0.11	**-0.32**	0.05		0.00	-0.03
	2km	pH	**0.48**	0.17	**0.46**	0.16	0.02	0.23	**-0.35**	**0.58**	**0.52**
		EC (µC/cm)	0.08	0.02	0.01	0.06	-0.12	**0.74**	-0.22	**0.36**	**0.58**
		DO (mg/L)	-0.15	0.04	-0.22	-0.03	-0.08	-0.11	-0.06	-0.28	**-0.40**
		Turb (ftu)	**0.72**	0.57	0.80	0.27	-0.18	-0.08	-0.17	0.13	0.05
		FL (mg/L)	-0.02	-0.01	-0.06	0.01	-0.11	**0.50**	-0.14	0.25	**0.68**
		NH$_3$-N (mg/L)	0.68	**0.52**	**0.73**	0.28	-0.21	0.05	-0.19	0.12	0.12
		NO$_3$--N (mg/L)	**0.39**	**0.73**	**0.50**	**0.45**	0.03	0.06	-0.14	-0.07	0.09
		PO$_4^{3-}$ (mg/L)	**0.52**	**0.36**	**0.53**	**0.33**	0.00	0.29	**-0.37**	**0.33**	**0.54**
		Chl_a (mg/L)	**0.56**	**0.31**	**0.63**	0.19	-0.27	0.17	0.04	0.17	0.23
		TN (mg/L)	0.08	-0.08	-0.05	-0.21	-0.28	-0.15	0.13	0.24	0.14
		COD (mg/L)	**0.45**	0.24	**0.45**	0.22	-0.08	**0.43**	-0.30	**0.32**	**0.52**

		TP (mg/L)	**0.42**	0.11	**0.42**	-0.01	-0.12	0.02	-0.15	**0.43**	0.19
		TARISS	-0.06	0.02	-0.27	**-0.40**	-0.34	-0.07		-0.04	0.03
		Taxon_R	-0.23	0.03	**-0.37**	-0.34	-0.16	-0.11		-0.05	0.05
(b)Circular buffer upstream the monitoring site	100m	pH	0.11							0.26	0.29
		EC (μC/cm)	0.05							-0.01	**0.49**
		DO (mg/L)	-0.06							-0.10	**-0.34**
		Turb (ftu)	-0.01							0.03	0.04
		FL (mg/L)	0.02							-0.07	**0.70**
		NH_3-N (mg/L)	0.09							-0.05	0.18
		NO_3--N (mg/L)	0.02							-0.08	0.03
		PO_4^{3-} (mg/L)	0.17							0.05	**0.33**
		Chl_a (mg/L)	0.09							0.02	0.16
		TN (mg/L)	-0.24							0.16	0.15
		COD (mg/L)	0.16							0.01	**0.39**
		TP (mg/L)	-0.07							0.25	0.03
		TARISS			-0.26					-0.10	-0.03
		Taxon_R			-0.26					-0.07	0.03
	500m	pH	**0.50**	0.20	**0.60**	-0.02	-0.08		-0.14	**0.54**	**0.64**
		EC (μC/cm)	**0.34**	0.19	**0.39**	0.19	-0.14		-0.04	0.28	**0.58**
		DO (mg/L)	**-0.32**	0.01	-0.26	-0.14	-0.02		-0.20	**-0.31**	**-0.42**
		Turb (ftu)	**0.57**	**0.37**	**0.71**	0.10	-0.01		-0.12	**0.44**	**0.56**
		FL (mg/L)	0.20	0.28	0.27	0.04	-0.12		-0.06	0.06	**0.39**
		NH_3-N (mg/L)	**0.58**	**0.37**	**0.73**	0.19	-0.13		-0.24	**0.41**	**0.67**
		NO_3--N (mg/L)	0.25	0.28	**0.36**	0.20	0.09		0.28	0.10	**0.46**
		PO_4^{3-} (mg/L)	**0.39**	**0.40**	**0.55**	0.20	-0.11		-0.06	**0.33**	**0.64**
		Chl_a (mg/L)	**0.37**	**0.37**	**0.62**	0.00	-0.09		0.10	0.28	**0.49**
		TN (mg/L)	-0.17	-0.24	0.02	0.00	-0.18		-0.05	0.03	0.11
		COD (mg/L)	**0.38**	**0.36**	**0.56**	0.10	0.06		-0.07	0.28	**0.58**
		TP (mg/L)	**0.34**	0.14	**0.50**	0.06	-0.17		0.17	**0.32**	**0.55**
		TARISS		-0.20	-0.13	0.09	**-0.38**		-0.04	-0.05	-0.05
		Taxon_R		-0.27	-0.23	0.19	-0.35		0.05	-0.05	-0.04
	1km	pH	**0.64**	0.25	**0.64**	-0.01	0.16		-0.22	**0.58**	**0.70**
		EC (μC/cm)	**0.46**	0.22	**0.41**	-0.04	0.27		-0.22	**0.42**	**0.63**
		DO (mg/L)	**-0.41**	0.00	-0.29	-0.02	-0.22		-0.13	-0.36	**-0.40**
		Turb (ftu)	**0.65**	**0.41**	**0.77**	0.07	0.23		-0.25	**0.43**	**0.59**
		FL (mg/L)	0.26	0.28	0.23	-0.15	0.31		-0.09	0.21	**0.49**
		NH_3-N (mg/L)	**0.64**	**0.48**	**0.80**	0.21	0.07		**-0.31**	**0.49**	**0.68**
		NO_3--N (mg/L)	**0.37**	**0.34**	**0.32**	0.05	**0.41**		0.02	0.21	**0.45**
		PO_4^{3-} (mg/L)	**0.54**	**0.39**	**0.61**	**0.03**	**0.39**		-0.23	**0.45**	**0.73**
		Chl_a (mg/L)	**0.46**	**0.39**	**0.60**	-0.04	0.13		-0.02	0.28	**0.50**
		TN (mg/L)	0.00	**-0.36**	0.06	-0.06	-0.16		0.02	0.17	0.10
		COD (mg/L)	**0.44**	**0.42**	**0.56**	-0.01	0.24		-0.13	0.33	**0.57**
		TP (mg/L)	**0.56**	0.22	**0.56**	-0.04	0.18		0.10	**0.47**	**0.62**
		TARISS	-0.10	-0.22	-0.09	-0.14	**-0.33**			0.05	0.09
		Taxon_R	-0.07	**-0.32**	-0.14	-0.08	-0.20			0.11	0.10
	2km	pH	**0.69**	**0.40**	**0.70**	0.20	0.10	0.08	-0.23	**0.70**	**0.70**
		EC (μC/cm)	**0.52**	**0.36**	**0.52**	**0.33**	0.24	0.11	**-0.44**	**0.51**	**0.64**
		DO (mg/L)	**-0.38**	-0.18	**-0.32**	-0.01	-0.15	-0.15	-0.15	**-0.41**	**-0.37**
		Turb (ftu)	**0.77**	**0.41**	**0.79**	0.03	0.26	-0.21	**-0.30**	**0.64**	**0.61**
		FL (mg/L)	**0.40**	**0.40**	**0.41**	**0.36**	0.23	0.21	-0.21	**0.35**	**0.54**
		NH_3-N (mg/L)	**0.79**	**0.51**	**0.83**	0.20	0.07	0.05	**-0.42**	**0.69**	**0.70**
		NO_3--N (mg/L)	**0.34**	**0.35**	**0.31**	0.18	0.24	-0.07	-0.27	0.25	**0.36**
		PO_4^{3-} (mg/L)	**0.67**	**0.50**	**0.74**	**0.33**	0.30	0.06	**-0.39**	**0.65**	**0.75**
		Chl_a (mg/L)	**0.59**	**0.44**	**0.63**	0.00	-0.02	0.30	-0.25	**0.52**	**0.56**
		TN (mg/L)	-0.04	-0.27	-0.06	-0.14	-0.18	-0.02	-0.22	0.07	-0.02
		COD (mg/L)	**0.55**	**0.44**	**0.58**	0.13	0.09	0.10	0.01	**0.51**	**0.59**
		TP (mg/L)	**0.57**	0.23	**0.54**	0.02	0.09	-0.14	-0.18	**0.55**	**0.65**
		TARISS	-0.08	-0.27	-0.08	-0.01	**-0.38**	-0.16		0.09	0.11
		Taxon_R	-0.07	-0.28	-0.09	0.05	-0.23	-0.18		0.10	0.09
(c) Entire watershed upstream the monitoring site		pH	**0.64**	**0.49**	**0.66**	**0.46**	0.36	-0.30	-0.13	**0.66**	**0.67**
		EC (μC/cm)	**0.64**	**0.69**	**0.47**	**0.48**	0.33	**-0.55**	**-0.40**	**0.64**	**0.70**
		DO (mg/L)	-0.29	-0.28	-0.28	-0.29	0.07	0.00	0.18	**-0.38**	-0.27
		Turb (ftu)	0.60	**0.36**	**0.73**	0.26	**0.40**	-0.22	0.08	**0.54**	**0.53**
		FL (mg/L)	**0.51**	**0.54**	**0.31**	**0.34**	**0.36**	**-0.38**	-0.23	**0.43**	**0.55**
		NH_3-N (mg/L)	**0.73**	**0.61**	**0.79**	**0.53**	0.17	-0.16	0.15	**0.70**	**0.71**
		NO_3--N (mg/L)	**0.45**	**0.58**	**0.30**	**0.43**	**0.41**	-0.25	-0.12	**0.44**	**0.42**
		PO_4^{3-} (mg/L)	**0.82**	**0.78**	**0.66**	**0.60**	**0.50**	-0.36	-0.08	**0.72**	**0.75**
		Chl_a (mg/L)	**0.61**	**0.58**	**0.67**	0.34	0.05	0.00	-0.11	**0.61**	**0.61**
		TN (mg/L)	-0.29	-0.11	-0.20	0.04	0.04	0.17	-0.02	-0.28	-0.25
		COD (mg/L)	**0.66**	**0.72**	**0.59**	**0.45**	-0.02	-0.20	-0.07	**0.74**	**0.72**
		TP (mg/L)	**0.45**	**0.41**	**0.49**	0.14	**0.18**	-0.29	**-0.32**	**0.57**	**0.50**

		TARISS	0.03	0.11	-0.10	0.05	0.29	**-0.32**	-0.23	0.10	0.06
		Taxon_R	0.02	0.04	-0.15	0.03	**0.34**	**-0.44**	-0.30	0.02	-0.03

Spatial method of land use estimation	**Spatial scale**	**Response Variable**	**Land use class**								
			IMC	**IBC**	**IBCM**	**WTL**	**UB**	**SVB**	**SRT**	**WR**	**AF**
(a)Circular buffer around the monitoring site	100m	pH	0.58	-0.50	0.44	-0.21		0.40	0.53		-0.70
		EC (µC/cm)	0.33	-0.52	0.46	-0.07		0.32	0.50		-0.39
		DO (mg/L)	-0.37	0.24	-0.05	0.16		-0.08	-0.44		0.52
		Turb (ftu)	0.66	-0.41	0.34	-0.21		0.36	0.53		-0.80
		FL (mg/L)	0.25	-0.44	0.23	-0.11		0.34	0.45		-0.23
		NH3-N (mg/L)	0.69	-0.61	0.36	0.04		0.37	0.54		-0.75
		NO3--N (mg/L)	0.29	-0.33	0.20	0.01		0.39	0.40		-0.29
		PO43- (mg/L)	0.59	-0.62	0.37	-0.16		0.45	0.60		-0.56
		Chl_a (mg/L)	0.55	-0.54	0.21	-0.21		0.28	0.46		-0.61
		TN (mg/L)	-0.30	0.13	-0.03	0.26		-0.23	-0.18		0.17
		COD (mg/L)	0.72	-0.42	0.22	-0.15		0.32	0.53		-0.74
		TP (mg/L)	0.37	-0.29	0.31	-0.12		0.21	0.45		-0.49
		TARISS	-0.28	-0.05	0.23			-0.20	-0.27		0.43
		Taxon_R	-0.33	-0.01	0.13			-0.23	-0.18		0.47
	500m	pH	0.63	-0.59	0.00	0.20	0.17	0.65	0.69	0.09	-0.75
		EC (µC/cm)	0.42	-0.53	0.22	-0.03	0.35	0.50	0.56	0.01	-0.40
		DO (mg/L)	-0.33	0.29	0.23	-0.01	-0.23	-0.41	-0.42	-0.02	0.45
		Turb (ftu)	0.77	-0.60	-0.12	0.40	0.05	0.78	0.76	-0.09	-0.80
		FL (mg/L)	0.29	-0.38	0.07	-0.21	0.25	0.29	0.37	0.01	-0.29
		NH3-N (mg/L)	0.75	-0.71	-0.01	0.38	0.17	0.81	0.80	0.11	-0.76
		NO3--N (mg/L)	0.32	-0.40	0.02	0.03	0.29	0.46	0.45	0.01	-0.43
		PO43- (mg/L)	0.62	-0.67	0.06	0.10	0.31	0.69	0.72	0.07	-0.65
		Chl_a (mg/L)	0.58	-0.68	-0.29	0.30	0.06	0.62	0.60	0.08	-0.62
		TN (mg/L)	-0.17	0.00	0.20	0.19	-0.07	-0.12	-0.11	-0.04	0.14
		COD (mg/L)	0.60	-0.55	-0.14	0.11	0.22	0.60	0.70	0.04	-0.64
		TP (mg/L)	0.44	-0.40	0.10	0.31	0.22	0.51	0.50	-0.01	-0.52
		TARISS	-0.43	0.07	0.45	-0.06	0.11	-0.21	-0.23		0.24
		Taxon_R	-0.43	0.11	0.47	-0.19	0.17	-0.24	-0.22		0.31
	1km	pH	0.60	-0.71	-0.05	0.53	0.02	0.56	0.74	0.09	-0.71
		EC (µC/cm)	0.51	-0.58	0.18	0.32	0.24	0.48	0.64	0.01	-0.48
		DO (mg/L)	-0.31	0.35	0.32	-0.21	0.15	-0.24	-0.44	-0.02	0.45
		Turb (ftu)	0.79	-0.71	-0.22	0.54	0.11	0.74	0.79	-0.09	-0.85
		FL (mg/L)	0.35	-0.43	0.05	0.14	0.34	0.29	0.44	0.01	-0.27
		NH3-N (mg/L)	0.79	-0.80	-0.08	0.47	0.26	0.75	0.81	0.11	-0.82
		NO3--N (mg/L)	0.44	-0.46	-0.04	0.16	0.20	0.42	0.49	0.01	-0.46
		PO43- (mg/L)	0.68	-0.76	0.02	0.38	0.34	0.66	0.80	0.07	-0.70
		Chl_a (mg/L)	0.60	-0.72	-0.30	0.40	0.07	0.53	0.62	0.08	-0.69
		TN (mg/L)	-0.18	0.08	0.15	0.16	-0.34	-0.14	-0.10	-0.04	0.21
		COD (mg/L)	0.61	-0.64	-0.25	0.33	0.13	0.51	0.68	0.04	-0.68
		TP (mg/L)	0.50	-0.51	0.04	0.51	0.18	0.48	0.57	-0.01	-0.54
		TARISS	-0.45	0.12	0.45	-0.10	0.07	-0.25	-0.20	0.01	0.25
		Taxon_R	-0.43	0.18	0.44	-0.17	0.06	-0.26	-0.15	-0.09	0.34
	2km	pH	0.58	-0.55	-0.05	0.54	0.19	0.44	0.59	-0.09	-0.45
		EC (µC/cm)	0.23	-0.40	0.24	0.13	-0.06	0.36	0.28	-0.12	-0.25
		DO (mg/L)	-0.40	0.17	0.42	-0.31	0.02	-0.22	-0.45	0.05	0.17
		Turb (ftu)	0.57	-0.48	-0.35	0.24	0.02	0.57	0.64	-0.09	-0.25
		FL (mg/L)	0.12	-0.29	0.15	0.13	-0.06	0.16	0.18	-0.09	-0.14
		NH3-N (mg/L)	0.60	-0.53	-0.31	0.16	0.01	0.64	0.66	-0.08	-0.26
		NO3--N (mg/L)	0.39	-0.19	-0.18	-0.04	0.04	0.40	0.13	-0.09	-0.29
		PO43- (mg/L)	0.68	-0.68	-0.08	0.24	0.00	0.68	0.68	-0.13	-0.41
		Chl_a (mg/L)	0.48	-0.52	-0.39	0.23	-0.06	0.55	0.69	-0.11	-0.06
		TN (mg/L)	-0.03	-0.09	0.10	0.28	0.24	-0.21	-0.04	0.06	0.11
		COD (mg/L)	0.55	-0.48	-0.17	0.28	-0.05	0.58	0.62	-0.21	-0.43
		TP (mg/L)	0.41	-0.38	-0.10	0.48	-0.03	0.36	0.49	-0.09	-0.27
		TARISS	-0.29	0.03	0.36	-0.09	-0.28	-0.25	-0.07	0.04	0.14
		Taxon_R	-0.26	0.07	0.36	-0.10	-0.34	-0.26	-0.05	0.114	0.22
(b)Circular buffer upstream the monitoring site		pH	0.45	-0.29	0.18	0.14		0.38	0.45		-0.53
		EC (µC/cm)	0.27	-0.38	0.26	0.00		0.41	0.26		-0.23
		DO (mg/L)	-0.39	0.16	0.18	0.05		-0.17	-0.33		0.30
		Turb (ftu)	0.53	-0.24	-0.15	0.53		0.13	0.32		-0.32
		FL (mg/L)	0.21	-0.33	0.19	-0.01		0.20	0.19		-0.16
		NH3-N (mg/L)	0.48	-0.31	-0.11	0.44		0.28	0.49		-0.32
		NO3--N (mg/L)	0.32	-0.02	-0.10	0.72		0.01	0.18		-0.30
		PO_4- (mg/L)	0.64	-0.53	0.09	0.30		0.25	0.60		-0.45
	100m	Chl_a (mg/L)	0.52	-0.44	-0.11	0.26		0.25	0.45		-0.22

		TN (mg/L)	-0.19	-0.10	0.17	-0.04		0.07	0.03		0.19
		COD (mg/L)	0.59	-0.38	0.09	0.21		0.35	0.51		-0.52
		TP (mg/L)	0.34	-0.15	0.11	0.09		0.02	0.23		-0.34
		TARISS	-0.18	0.02	0.08	0.11		-0.02	-0.12		0.44
		Taxon_R	-0.16	-0.03	0.06	-0.07		-0.03	-0.14		0.47
		pH	0.52	-0.40	0.13	0.29	-0.02	0.59	0.64		-0.63
		EC (μC/cm)	0.49	-0.35	0.26	0.05	0.19	0.45	0.60		-0.35
		DO (mg/L)	-0.29	0.18	0.18	-0.19	-0.14	-0.23	-0.38		0.33
		Turb (ftu)	0.72	-0.45	-0.08	0.47	0.10	0.76	0.73		-0.77
		FL (mg/L)	0.31	-0.29	0.11	-0.04	0.04	0.27	0.39		-0.17
		NH3-N (mg/L)	0.76	-0.68	0.08	0.33	0.19	0.77	0.80		-0.67
		NO3--N (mg/L)	0.41	-0.26	0.03	-0.01	0.20	0.45	0.50		-0.47
		PO43- (mg/L)	0.63	-0.49	0.12	0.14	0.20	0.64	0.74		-0.56
		Chl_a (mg/L)	0.56	-0.64	-0.20	0.34	0.00	0.58	0.61		-0.54
		TN (mg/L)	-0.23	-0.04	0.16	0.05	0.00	-0.11	-0.07		0.13
		COD (mg/L)	0.59	-0.43	-0.05	0.20	0.10	0.55	0.66		-0.53
		TP (mg/L)	0.47	-0.32	0.18	0.26	0.06	0.57	0.58		-0.44
		TARISS	-0.43	0.09	0.50	-0.18	0.09	-0.17	-0.26		0.38
		Taxon_R	-0.42	0.15	0.45	-0.19	0.19	-0.21	-0.23		0.51
	1km	pH	0.64	-0.49	0.09	0.37	-0.08	0.59	0.68	0.21	-0.68
		EC (μC/cm)	0.54	-0.43	0.32	0.22	-0.01	0.47	0.65	-0.11	-0.47
		DO (mg/L)	-0.37	0.27	0.15	-0.21	0.12	-0.24	-0.43	0.06	0.45
		Turb (ftu)	0.81	-0.48	-0.11	0.70	0.06	0.72	0.74	0.14	-0.71
		FL (mg/L)	0.32	-0.38	0.18	0.15	-0.04	0.32	0.45	-0.12	-0.23
		NH3-N (mg/L)	0.81	-0.66	0.04	0.55	0.19	0.76	0.80	0.09	-0.76
		NO3--N (mg/L)	0.46	-0.28	0.07	0.14	-0.03	0.42	0.53	0.07	-0.41
		PO43- (mg/L)	0.73	-0.57	0.11	0.38	-0.02	0.67	0.80	0.02	-0.68
		Chl_a (mg/L)	0.64	-0.69	-0.23	0.49	-0.02	0.52	0.60	-0.02	-0.58
		TN (mg/L)	-0.17	-0.03	0.16	-0.06	-0.24	-0.08	-0.06	0.21	0.10
		COD (mg/L)	0.63	-0.43	-0.03	0.34	-0.07	0.49	0.66	-0.10	-0.62
		TP (mg/L)	0.56	-0.40	0.16	0.51	-0.07	0.55	0.55	0.00	-0.50
		TARISS	-0.30	0.00	0.37	-0.23	-0.25	-0.15	-0.12	0.14	0.14
		Taxon_R	-0.28	0.06	0.38	-0.17	-0.21	-0.17	-0.09	0.05	0.21
	2km	pH	0.63	-0.43	0.30	0.70	0.37	0.75	0.73	0.52	-0.69
		EC (μC/cm)	0.57	-0.40	0.47	0.50	0.49	0.65	0.66	0.26	-0.50
		DO (mg/L)	-0.32	0.30	-0.06	-0.45	-0.27	-0.37	-0.40	-0.20	0.41
		Turb (ftu)	0.72	-0.36	0.18	0.80	0.23	0.70	0.77	0.31	-0.72
		FL (mg/L)	0.47	-0.44	0.35	0.36	0.44	0.55	0.51	0.34	-0.25
		NH3-N (mg/L)	0.73	-0.53	0.24	0.76	0.36	0.77	0.82	0.33	-0.78
		NO3--N (mg/L)	0.45	-0.19	0.21	0.29	0.35	0.42	0.45	0.29	-0.47
		PO43- (mg/L)	0.71	-0.52	0.33	0.68	0.44	0.78	0.83	0.50	-0.69
		Chl_a (mg/L)	0.55	-0.71	0.02	0.69	0.29	0.58	0.64	0.38	-0.62
		TN (mg/L)	-0.19	0.00	-0.03	-0.06	-0.16	-0.06	-0.12	0.09	-0.01
		COD (mg/L)	0.59	-0.38	0.18	0.57	0.31	0.59	0.68	0.32	-0.63
		TP (mg/L)	0.58	-0.38	0.32	0.66	0.42	0.55	0.58	0.29	-0.58
		TARISS	-0.32	-0.14	0.06	-0.03	-0.10	-0.07	-0.03	0.00	0.08
		Taxon_R	-0.34	-0.10	0.11	-0.03	-0.11	-0.08	-0.03	-0.10	0.18
(c) Entire watershed upstream the monitoring site		pH	0.58	0.08	0.53	0.57	0.58	0.66	0.71	0.57	-0.59
		EC (μC/cm)	0.52	-0.16	0.71	0.38	0.48	0.65	0.76	0.49	-0.46
		DO (mg/L)	-0.25	-0.10	-0.13	-0.41	-0.40	-0.47	-0.36	-0.25	0.31
		Turb (ftu)	0.57	0.47	0.30	0.71	0.32	0.43	0.57	0.26	-0.48
		FL (mg/L)	0.28	-0.31	0.58	0.23	0.37	0.50	0.58	0.51	-0.27
		NH3-N (mg/L)	0.71	0.20	0.48	0.69	0.51	0.62	0.71	0.46	-0.63
		NO3--N (mg/L)	0.32	-0.03	0.41	0.32	0.34	0.55	0.55	0.44	-0.26
		PO43- (mg/L)	0.59	-0.08	0.63	0.59	0.62	0.74	0.84	0.62	-0.53
		Chl_a (mg/L)	0.53	-0.08	0.38	0.77	0.48	0.52	0.61	0.40	-0.50
		TN (mg/L)	-0.25	0.09	-0.32	-0.09	-0.05	-0.29	-0.30	-0.04	0.11
		COD (mg/L)	0.70	0.07	0.62	0.63	0.68	0.71	0.75	0.50	-0.71
		TP (mg/L)	0.42	0.04	0.46	0.69	0.27	0.49	0.54	0.21	-0.37
		TARISS	0.00	-0.24	0.25	-0.03	0.11	0.01	0.10	0.09	0.03
		Taxon_R	-0.06	-0.24	0.16	-0.09	0.06	-0.03	0.07	-0.01	0.12

Table S4. A table showing land-use variables that were retained by the forward selection in the RDA models for (a) water quality and (b) macroinvertebrates. The models were constructed using the three different land use estimators (i.e. circular buffer around monitoring site, circular buffer upstream the monitoring site, and entire watershed area upstream the monitoring site) incorporating land use at different spatial scales (i.e. 100m, 500m, 1km and 2km)

RDA Models	**Land use class**	**Circular buffer around the monitoring site**				**Circular buffer upstream the monitoring site**				**Entire watershed upstream the monitoring site**
		100 m	**500 m**	**1k m**	**2k m**	**100 m**	**500 m**	**1k m**	**2k m**	
(a)Water quality	Grazed Shrub land									✓
	Grazed Grassland			✓						
	Barren Land				✓			✓	✓	
	Sparse Vegetation									
	Irrigated Maize									
	Afro Alpine Forest		✓	✓	✓					
	Subalpine Forest									
	Grazed Woodland									
	Protected Woodland/Bushland	✓	✓	✓	✓	✓	✓	✓		
	Irrigated Mixed Crops	✓								
	Irrigated Banana and Coffee								✓	
	Irrigated Banana, Coffee and Maize									
	Wetland									
	Urban Buildings									
	Sparse Vegetation or Bare land	✓	✓			✓	✓			✓
	Shrub land or/ and Thickets			✓			✓			
	Water							✓	✓	✓
	Afromontane Forest (dense forest)									
	Grazed Shrub land									
(b)Macroinvertebrate	Grazed Grass land									
	Barren Land					✓				
	Sparse Vegetation				✓	✓			✓	
	Irrigated Maize				✓		✓		✓	

	Afro Alpine Forest						✓			
	Subalpine Forest									
	Grazed Wood land							✓		
	Protected Woodland/Bushland							✓		
	Irrigated Mixed Crops									
	Irrigated Banana and Coffee									
	Irrigated Banana, Coffee and Maize									
	Wetland									
	Urban Buildings									
	Sparse Vegetation or Bare land									
	Shrub land or/ and Thickets									
	Water		✓			✓				
	Afromontane Forest (dense forest)	✓	✓	✓	✓	✓	✓	✓	✓	

Table S5. A table showing land-use variables that were retained in the generalized linear models by backward and forward selection procedure for (a) taxon richness, (b) TARISS score, and (Chao-1). The models were constructed using the three different land use estimators (i.e. circular buffer around the monitoring site, circular buffer upstream the monitoring site, and entire watershed area upstream the monitoring site) incorporating land-use at different spatial scales (i.e. 100m, 500m, 1km and 2km).

Generalized Linear Models		**Circular buffer around the monitoring site**				**Circular buffer upstream the monitoring site**				**Entire watershed upstream the monitoring site**
	Land use class	**100 m**	**500 m**	**1k m**	**2k m**	**100 m**	**500 m**	**1k m**	**2k m**	
(a) Taxon Richness	Grazed Shrub land	✓		✓						
	Grazed Grassland		✓						✓	✓
	Barren Land					✓	✓			
	Sparse Vegetation			✓	✓			✓		
	Irrigated Maize	✓	✓							
	Afro Alpine Forest					✓				
	Subalpine Forest				✓		✓		✓	✓
	Grazed Woodland			✓				✓	✓	✓
	Protected Woodland/Bushland		✓						✓	✓
	Irrigated Mixed Crops									✓
	Irrigated Banana and Coffee			✓		✓	✓	✓	✓	✓
	Irrigated Banana, Coffee and Maize		✓		✓					
	Wetland								✓	✓
	Urban Buildings			✓			✓		✓	✓
	Sparse Vegetation or Bare land	✓					✓	✓		
	Shrub land or/ and Thickets		✓		✓	✓				
	Water				✓		✓	✓		
	Afromontane Forest (dense forest)	✓		✓	✓				✓	✓
(b)TARISS	Grazed Shrub land				✓		✓		✓	✓
	Grazed Grassland	✓	✓					✓		✓
	Barren Land		✓							

	Sparse Vegetation				✓	✓	✓			
	Rain Fed Maize			✓				✓	✓	✓
	Irrigated Maize					✓	✓			
	Afro Alpine Forest			✓					✓	✓
	Subalpine Forest						✓			
	Subalpine Bushland		✓		✓					
	Grazed Woodland							✓	✓	✓
	Protected Woodland/Bushland	✓							✓	✓
	Irrigated Mixed Crops	✓			✓	✓	✓			
	Irrigated Banana and Coffee		✓							
	Irrigated Banana, Coffee and Maize			✓				✓	✓	✓
	Wetland		✓				✓		✓	✓
	Urban Buildings				✓					✓
	Sparse Vegetation or Bare land	✓		✓			✓		✓	✓
	Shrub land or/ and Thickets							✓	✓	✓
	Water									
	Afromontane Forest (dense forest)	✓	✓	✓	✓	✓			✓	✓
Chao-1	Grazed Shrub land						✓			✓
	Grazed Grassland		✓		✓			✓	✓	
	Barren Land									
	Sparse Vegetation						✓			
	Rain Fed Maize			✓			✓		✓	✓
	Irrigated Maize			✓		✓	✓			✓
	Afro Alpine Forest			✓	✓				✓	
	Subalpine Forest		✓					✓		
	Subalpine Bushland		✓		✓					
	Grazed Woodland							✓	✓	✓

	Protected Woodland/Bushland	✓							✓	✓
	Irrigated Mixed Crops	✓		✓	✓	✓	✓			✓
	Irrigated Banana and Coffee		✓							
	Irrigated Banana, Coffee and Maize	✓				✓		✓	✓	✓
	Wetland				✓					
	Urban Buildings						✓			✓
	Sparse Vegetation or Bare land				✓			✓		✓
	Shrub land or/ and Thickets			✓				✓	✓	
	Water									
	Afromontane Forest (dense forest)		✓	✓	✓		✓	✓	✓	✓

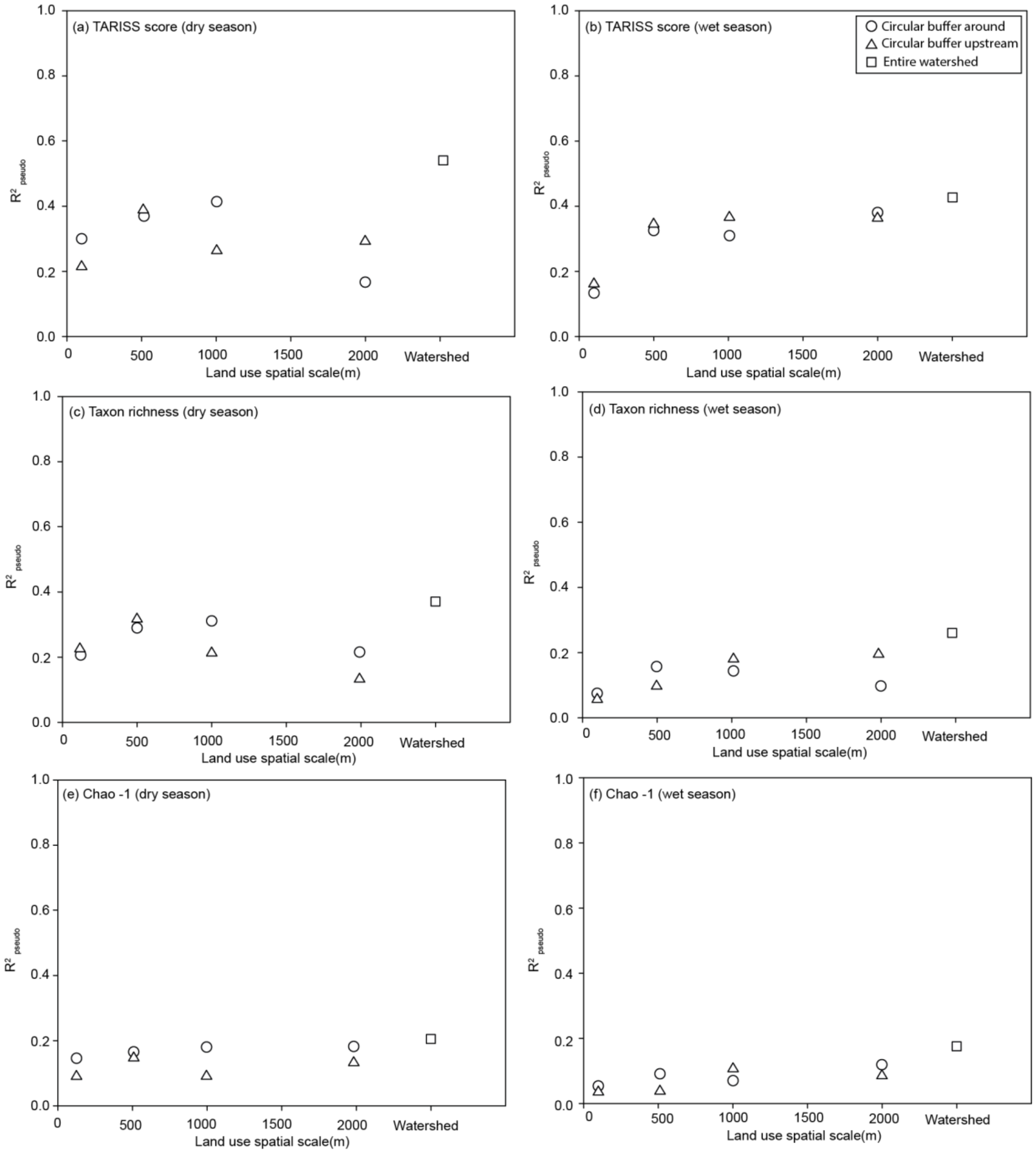

Fig. S1. Variation in TARISS score (a and b), taxon richness (c and d), and Chao-1 (e and f) explained by generalized linear models (R^2_{pseudo}) that are based on three different types of land-use estimators (i.e., circle: circular buffer around the monitoring site, triangle: circular buffer upstream the monitoring site, and square: entire watershed area upstream the monitoring site) at different spatial scales (i.e., 100m, 500m,1km and 2km) in the dry and wet seasons.

Chapter 3

Using spatial-stream-network (SSN) models to understand the spatial patterns and predict dynamics of stream water chemistry and benthic macroinvertebrates at catchment scale: A case study in the Usa-Kikuletwa River catchment

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Abstract

The unique branching geometry of river networks distinguishes riverine systems from other ecological networks and influences key ecological processes in these systems. However, the application of suitable models that account for the specific dendritic structure and flow-direction in examining key physical, chemical, and biological processes in river systems is still incipient. We applied a spatial stream network (SSN) model that aptly integrates dendritic features (network topology, directionality) to scrutinize the spatial patterns of benthic macroinvertebrates and water chemistry at the catchment scale. The model components described spatial dependencies as a function of hydrologic distances between flow-connected (tail-up model) and flow-unconnected (tail-down model), and straight-line distances (Euclidean model) between sites. We used water chemistry (i.e., fluoride, total nitrogen, and total phosphorus) and macroinvertebrate indices data from forty monitoring sites spread across the Usa-Kikuletwa River catchment, northeastern Tanzania. We found that spatial autocorrelation exists in water chemistry variables and macroinvertebrate indices at both fine- and broad- spatial scale and that SSN models managed to make good predictions of water chemistry concentrations and macroinvertebrate indices with estimates of uncertainty. SSN models showed that variation in water chemistry variables was largely accounted for by broad-scale tail-up models suggesting the effects of hydrological transport and upstream dependence of water chemistry variables. The tail-down relationships captured a larger portion of macroinvertebrate indices variance suggesting that many sites may be connected by dispersal (adults or propagules), drift or by broad-scale landscape characteristics that have control over channel morphology and hydrologic patterns. The differences in spatial dependence indicate that stream water chemistry and macroinvertebrate indices are influenced by diverse ecological processes acting at different spatial scales. Overall, our study highlights the value of SSN models to examine the spatial patterns of stream water chemistry and macroinvertebrate indices and stress the need to specify spatial dependencies representing the dendritic network structure of river ecosystems. More importantly, spatial stream network models could be used to support river basin management in the region: inferences about regional river conditions can be generated and thus can be used to locate potentially impaired river segments in a rapid and cost-effective way.

Key words: Dendritic Ecological Network (DEN); spatial autocorrelation; hydrological distance; Spatial Stream Network (SSN) models; connectivity; river networks.

1. Introduction

Rivers are spatially organized into hierarchic dendritic networks consisting of headwater streams connected by larger mainstem channels (Fagan, 2002; Grant et al., 2007; Brown and Swan, 2010; Seymour et al., 2015; Tonkin et al., 2018). The characteristic physical network structure and longitudinal continuity of river systems differentiates them from many other ecological networks and influences the physical, chemical and biological processes in these systems (Benda et al., 2004; Ganio et al., 2005; Grant et al., 2009; Brown and Swan, 2010; Peterson et al., 2013). For example, the diversity of instream habitats such as substrate size and woody debris is expected to be higher near confluences (i.e., locations where stream segments converge) within a dendritic network compared with a lattice network (i.e., nodes and edges are discrete features, with nodes as habitat and edges as functional links between habitat patches) because segments of different size converge resulting in disturbance and environmental heterogeneity (Benda, 2008).‘Dendritic’ describes the geometric pattern of arborescent bifurcation, consisting of a ‘mainstem’ and ‘branches’ which decrease in size and increase in number hierarchically as one proceeds upwards through the network (Grant et al., 2007). Dendritic ecological networks (DENs) are unique in that both nodes (patches) and edges (branches) are potential habitats, and local habitats lack distinct boundaries (e.g., streams are continuums of shallower riffles and deeper pools)(Grant et al., 2007). In addition, the movement of organisms, material and energy is mainly constrained to the physical networks, which forms ecological corridors (Ganio et al., 2005; Peterson et al., 2013; Isaak et al., 2014).

Standard statistical methods commonly used to examine DEN data normally ignore the network structure, connectivity, and directionality of the network, or assume that proximity and connectivity are adequately described using Euclidean distance (Peterson et al., 2013; Isaak et al., 2014). When these methods are used the implicit assumption is that topological relationships within the network are unimportant (Peterson et al., 2013). Consequently, given the unique characteristics of DENs and the spatial complexity of processes on the physical network, statistical methods used to quantify relationships in other ecological networks may not appropriately represent the influence of network structure and connectivity on physical, chemical and biological processes in these systems (Fagan, 2002; Grant et al., 2007; Peterson et al., 2013). For example, most of the spatial statistical techniques applied to data measured on river networks were developed for terrestrial applications and are not optimized for river systems. However, the branching geometry of river networks and unidirectional flow of water distinguish riverine systems from their terrestrial counterparts and influences the ecological patterns and processes in these systems (Ganio et al., 2005; Grant et al., 2009; Brown and Swan, 2010; Peterson et al., 2013). As such, spatial statistical methods need to account for the unique properties of stream networks if they are to be optimized for stream data.

Spatial autocorrelation (i.e., non-independence among observations) is the tendency for measurements of an attribute to show a pattern of similarity relative to the distance separating them (Legendre, 1993; Isaak et al., 2014). Tobler's first law of geography states that: ‘‘everything is related to everything else, but near things are more related than distant things’’(Tobler, 1970). Spatial autocorrelation is inherent in ecological data sets and occurs in both aquatic and terrestrial systems at multiple scales (Legendre, 1993; Koenig, 1999; Peterson and Ver Hoef, 2010). Spatial autocorrelations is complex in river systems as the intensity varies with the connectivity and directionality within the network (Isaak et al., 2014). However, classical statistical techniques assume that each measurement is independent of others and contains non-redundant information (Isaak et al., 2014). In reality, biological or environmental values observed at a given site are not independent of values in more or less distant neighboring sites. The lack of consideration of this in classical statistical analysis is a potential source of misleading results in ecological analyses (Legendre, 1993; Bonada et al., 2012). In river systems, for example, nested watersheds and flow connectivity may produce spatial autocorrelation patterns that are not captured by Euclidean distance (Erin E Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010) (see Fig.1. a hypothetical illustration of spatial patterns in river network). In addition, given that certain sampling locations often occur closer in space than others, the statistical assumption of independence among observations may be violated, and poor parameter estimation and statistical inference could result (Ganio et al., 2005; Isaak et al., 2014). Consequently, spatially explicit statistical frameworks that integrate the branching geometry of the river networks and account for spatial autocorrelation are needed to better understand the key physical, chemical and biological processes in river systems (Grant et al., 2007; Peterson and Ver-Hoef, 2010; Peterson et al., 2013; Isaak et al., 2014).

Developments in geostatistical modeling provide a valuable new perspective on stream networks by revealing hydrological and ecological patterns in a spatially continuous manner (Ver Hoef and Peterson, 2010; Mcguire et al., 2014). Recently, a new class of geostatistical (i.e., spatial stream-network (SSN) models, based on valid covariance structures for stream networks has been developed (Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010). The covariance structures account for the unique properties of stream networks such as a dendritic structure, connectivity, directed flow, and abrupt changes near tributary confluences (Peterson and Ver-Hoef, 2010; Isaak et al., 2014). The SSN models use a combination of ‘flow-connected’ and ‘flow-unconnected’ distances (i.e., spatial relationships based on hydrologic distance), and Euclidean distance (i.e., across catchment) to estimate the spatial relationships between stream sites. In this way, SSN models can account for spatial autocorrelation that may arise in stream networks due to both passive (e.g., downstream transport of nutrients and macroinvertebrates by drift) and active (e.g., upstream migration of fish and macroinvertebrates) interactions with the flow (Peterson and Ver-Hoef, 2010; Ver-Hoef and Peterson, 2010; Isaak et al., 2014). Moreover, SSN models can be used with various types of stream data (e.g., habitat conditions, water quality, biological attributes) through the application of appropriate statistical distributions (e.g., Gaussian, binomial, Poisson) (Isaak et al., 2014).

Despite the obvious recognition that the spatial configuration of river networks can be an important determinant of ecosystem functioning, very few studies have explicitly considered the use of SSN models for studying various ecological phenomena in river systems (e.g., Gardner and Mcglynn, 2009; Frieden et al., 2014; Jones et al., 2014; Isaak et al., 2017; Jackson et al., 2018). These studies have revealed the strength of the branching geometry of the river networks in regulating numerous physical, chemical, and biological processes. They also found that the spatial models performed significantly better than the non-spatial models (Isaak et al., 2017; Jones et al., 2014). This highlights that a more spatially explicit examination of stream networks is needed, particularly in different watersheds and regions.

Earlier studies on the application of SSN models are restricted to temperate regions with rivers having permanent water flow (e.g., Peterson and Urquhart, 2006; Jones et al., 2014; Mcguire et al., 2014; Isaak et al., 2017; Scown et al., 2017; Neill et al., 2018; Larsen et al., 2019), but no studies have been conducted in (sub) tropical Africa where water flow patterns are highly variable. Additionally, most temperate studies have found spatial dependence of stream-water chemistry to be largely structured by flow-directionality, however, differences might arise in this type of tropical river system because of the unique geomorphic characteristics of each river basin that influences the spatial patterns of the stream and river attributes. Furthermore, to the authors' knowledge, there is no earlier study where a SSN model has been applied to stream fluoride data, and only one study for macroinvertebrate data (i.e., Frieden et al., 2014), making this study of the generic importance beyond the study system.

In this study, we scrutinize the role of stream network structure in determining the spatial patterns (variation and distribution) of benthic macroinvertebrates and water chemistry at the catchment scale using SSN models. We make use of a data set of water chemistry (i.e., fluoride, total nitrogen, and total phosphorus) and benthic macroinvertebrate indices (i.e., Taxon richness and TARISS) collected at forty monitoring sites in the Usa-Kikuletwa River catchment (UKRC) in northeastern Tanzania. We used fluoride, total nitrogen, and total phosphorus as our focal ions because fluoride is a natural occurring pollutant in the study area (Selemani et al., 2017; Chacha et al., 2018; Kitalika et al., 2018), and total nitrogen and total phosphorus are pollutants linked to agricultural activities: a main anthropogenic activity affecting river systems in the region (PBWO/IUCN, 2007; Mwaijengo et al., 2020). TARISS is a macroinvertebrate biotic index developed for assessing the ecological condition of river systems in the country. Our objectives were (i) to establish the spatial patterns and spatial autocorrelation in water chemistry variables and macroinvertebrate indices in the UKRC using SSN models, and determine the spatial distances (range) over which these spatial relationships are expressed, and (ii) to use the SSN models to accurately predict water chemistry concentrations and benthic macroinvertebrate indices (at unobserved/ un-sampled locations) across the UKRC. We expect spatial dependence of stream water chemistry to be structured by flow-directionality and topology of the river network. This is in line with the linear concept of nutrient enrichment along the stream gradient, from the upper to the lower reaches (i.e., river continuum, Vannote et al.,1980). On the other hand, longitudinally (i.e., along the river's trajectory) patchiness in the stream network may arise because of the local influences of landscape features such as geology and localized input of pollutants (especially point sources of concentrated pollution such as flower farms).

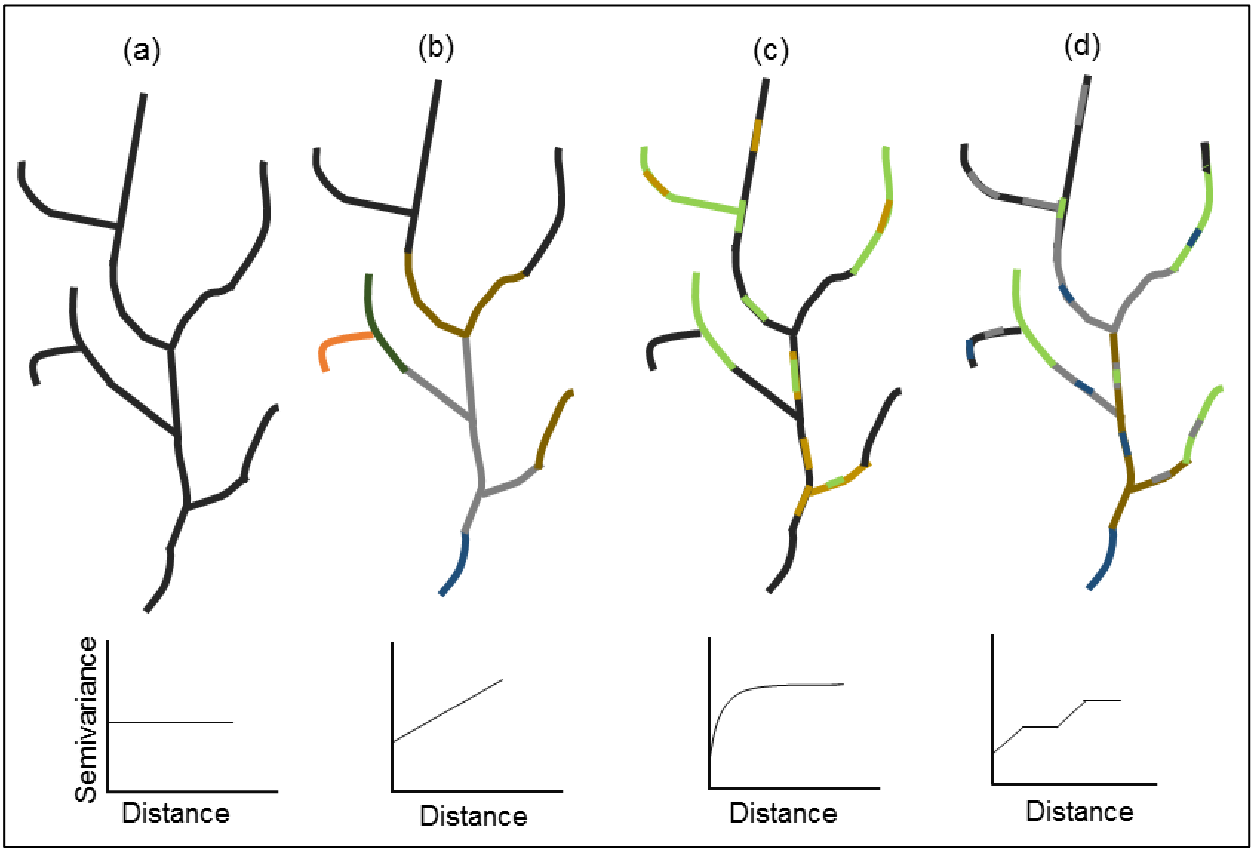

Fig. 1. A hypothetical illustration of the spatial patterns of a variable (e.g., concentrations of total phosphorus) mapped along a river network and the associated semivariograms. In (a), there is no spatial structure in the variance at the sampled scale. In (b), spatial dependency at a broad scale reflects a single dominant gradient of variation from upstream to downstream. A gradient symbolized in the network map by changes in line color from the upper left (black) to the lower right (blue) of the stream network. In (c), small-scale heterogeneity reflects patchiness and discontinuity where, for example, factors influencing the variable operate at fine scales, and the range is reached over shorter distances resulting in a faster saturation of the semivariogram. In (d), nested heterogeneity reflects a combination of small-scale patchiness embedded in a broad-scale gradient (with multiple inflection points). In this case, patterns are influenced by factors operating at multiple scales. The semivariance is simply half the

variance of the differences between all possible points spaced a constant distance apart. The figure is re-drawn after Mcguire et al. (2014).

2. Materials and Methods

2.1. Study Area

The study was conducted in the Usa-Kikuletwa River Catchment (Fig. 2) which is located along 36°43'0"E to 36° 57' 0" E Longitude and 3°14'0"S to 3°33'0"S Latitude in the Upper Pangani River Basin (UPRB), northeastern Tanzania. The Usa-Kikuletwa River catchment has a semi-arid climate, with an annual mean temperature of 21°C and average annual precipitation of approximately 2500 mm in the highlands and around 500 mm in the lowland (NSCA, 2007). The catchment experiences two rainy seasons: the long rains (*masika*) from March through May and the short rains (*vuli*) which are less reliable normally coming in November and December; the dry season (*kiangazi*) is from June to October (Kiptala et al., 2013). The drainage area of the Usa-Kikuletwa River is about 271 km^2, and the main river channel is 40 km long. The river sources are perennial springs along the slopes of Mt. Meru (4,565 m.a.s.l.).

Agriculture and pastoralism are the primary livelihood activities in the catchment, contributing to about 70% of the household income (Meru District Council, 2013). Agroforestry and Afro-alpine forest form the dominant land-use types in the upper reaches (PBWO/IUCN, 2007; Kiptala et al., 2013). Large scale commercial flower farming is practiced in the middle reach, which results in river water abstraction for irrigation purposes (PBWO/IUCN, 2007). The lower reaches of the catchment wind their way through a dry landscape where the human population is sparse. Land-use is dominated by irrigation agriculture (maize, beans, rice, tomatoes, and other vegetables), free grazing, shrub land, and grassland (Kiptala et al., 2013; Mwaijengo et al., 2020).

In total, forty sites were monitored from streams/ rivers that flow into four major river systems: Malala River, Tengeru River, Usa River, and Maji ya chai River, which drain to form the Usa-Kikuletwa catchment. The sites capture the latitudinal spatial arrangement of the river networks and land-use activities from upstream to downstream.

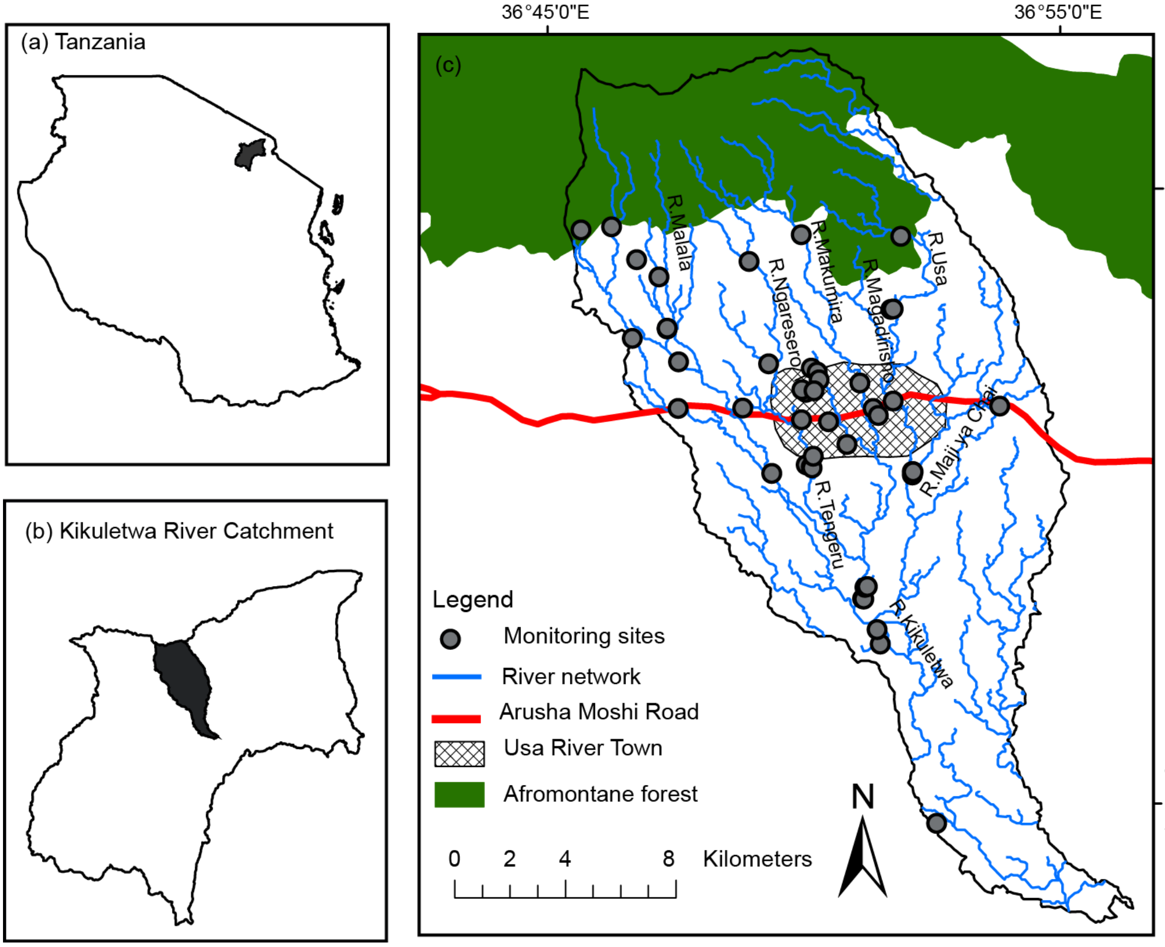

Fig.2. Map of the Usa-Kikuletwa River catchment showing the location of the forty monitoring sites: Insert: (a) map of Tanzania with the location of the Kikuletwa River catchment, and (b) map of Kikuletwa River catchment with the location of the Usa-Kikuletwa River catchment.

2.2 Data Collection

Water samples were collected from forty monitoring sites (Fig.2). The water samples were collected by inserting clean bottles of 1-litre at the mid-width of the river to an about 30-cm depth below the water surface in the opposite direction of the current flow of the river (APHA, 2012). The samples were transported in an iced cooler box to the laboratory of the Department of Water Environmental Science and Engineering at the Nelson Mandela African Institution of Science and Technology (NM-AIST), Arusha for analysis. The samples were stored at 4 °C until ready for analysis. Chemical measurements of total phosphorus (TP) and total nitrogen (TN) were carried out in the laboratory using a portable spectrophotometer (Model HACH-DR 2800). Total phosphorus concentration was measured using PhosVer3 with the acid persulfate digestion method (range: 0.06 to 3.50 mg/L PO_4^{3-}), and total nitrogen was measured using a persulfate digestion method (range: 0.1 to 25.0 mg/L N). Fluoride (F-) was measured using an ion-selective electrode (Mettler Toledo SevenCompact™ pH/Ion S220). Storage and chemical analyses followed the standard methods for the examination of water and wastewater by APHA (2012).

Macroinvertebrates were collected in a semi-quantitative way using a kick net of 1mm mesh size on a 30-cm square frame following the Tanzania River Scoring System (TARISS) method (Kaaya et al., 2015). The macroinvertebrates were sampled from the dominant habitat type present at each site (i.e., the habitat that covers about 70% of the 50 m stretch making up the river section at the site). Sampled habitat types included (i) stones in-current (cobbles, boulders and bedrock), (ii) vegetation/macrophyte, and (iii) gravel/ sand/mud (GSM). Stones and GSM habitats were sampled for one minute by kicking, turning, or scraping them with the feet, whilst continuously sweeping the net through the disturbed area. The vegetation/ macrophyte habitat was sampled by pushing the net vigorously and repeatedly against and through the vegetation over an area of approximately two meters. All drifting material collected in the kick net was stored in a labeled plastic container with 70% ethanol and transported to the laboratory for sorting and identification. Macroinvertebrates were identified with a dissecting microscope (10X magnification) to family level using different identification keys (Croft, 1986; Davies and Day, 1998; Gerber and Gabriel, 2002).

We calculated two macroinvertebrate biotic indices i.e., taxon richness, the TARISS score, and taxon turnover from the macroinvertebrate counts. The TARISS index was developed specifically for river macroinvertebrates in Tanzania: designed for assessing the ecological condition and the cumulative anthropogenic impacts (including those related to catchment land-use, riparian composition and condition, channel condition and form, and in-stream habitat) on river systems in the country. It takes high values when a site contains many sensitive taxa. The index was calculated following (Kaaya et al., 2015) by summing up taxon-specific sensitivity weighting scores for each site. This index, therefore, does not consider the abundance. The sensitivity weighting ranges from 1 to 15, with values >10 indicating taxa less tolerant to pollution. For taxon turnover, macroinvertebrate abundances we first transformed to a Bray Curtis distance and next principal coordinates analysis (PCoA) was performed using the *Capscale* function in R. The sites score along the first PCoA axis was then used as a response variable in the SSN models.

2.3 GIS analysis

We generated spatial data needed for spatial stream-network modelling in ArcGIS version 10.2.2 (ESRI Company, Redlands, California, USA). We used the Spatial Tools for the Analysis of River Systems (STARS) to construct a landscape network, which is a spatial data structure designed to store topological relationships between nodes (confluences), directed edges (stream segments), and polygons (Peterson and Ver Hoef, 2014). The spatial information included the hydrologic distances and spatial weights (i.e., quantify the spatial relationships that exist among features in the given locations) which are based on watershed area, as well as, watershed-scale land-use and topographic characteristics for each observed site. We calculated the spatial weights by locating every confluence in the stream network and weighting each segment in proportion to its watershed area (which was used as a surrogate for discharge), where weights summed to 1. Spatial weights are generated using metrics that represent the relative influence of one site on another to create more ecologically representative distance measures (Ver Hoef et al., 2006). For a detailed description of the GIS methodology, see Peterson and Ver Hoef, 2014.

In order to make predictions of the instream attributes at unsampled sites, we created 110 prediction sites for the entire Usa-Kikuletwa catchment in ArcGIS. We used the STAR tool to generate spatial information including the hydrologic distances and spatial weights which are based on watershed area, as well as, watershed-scale land-use and topographic characteristics for each prediction site.

2.4 Covariance models and spatial-weighting schemes

Two classes of auto-covariance (i.e., autocorrelation) functions have been developed to represent spatial relationships in streams: the tail-up (i.e., upstream direction) and tail-down (i.e., downstream direction) models (Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010). The models are based on moving-average (MA) constructions and assume that the stream network is dendritic and not braided (Isaak et al., 2014). These models account for two types of spatial relationships based on hydrologic distance (i.e., flow-connected and flow-unconnected), rather than Euclidean distance. Two locations are considered flow-connected if water flows from an upstream location to a downstream location (Fig.3 a, b). In contrast, two locations are considered flow-unconnected when they reside on the same stream network (e.g., share a common confluence downstream), but do not share flow (Peterson and Ver Hoef, 2010; Peterson et al., 2013) (Fig.3 c, d). Spatial autocorrelation occurs between sites when the MA functions overlap, with greater autocorrelation resulting from greater overlap (Peterson and Ver Hoef, 2010). The tail-up and tail-down models differ in the way they represent flow-connected and flow-unconnected spatial relationships in the spatial stream-network model. In the tail-up models, the MA function points in the upstream direction, as a result, spatial autocorrelation is only permitted between flow-connected sites (Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010) (Fig. 3 a, c). Spatial weights are used to split the tail-up MA function at confluences based on flow volume, watershed area, or other relevant attributes, which allows tributary influences on down-stream conditions to be correctly represented (Isaak et al., 2014) The moving-average function for the tail-down model, in contrast, points in the downstream direction, and so spatial correlation is allowed between both flow-connected and flow- unconnected sites (Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010) (Fig.3 b, d). As such, the tail-up models may be useful for modelling materials such as water chemistry, temperature, sediment, or organisms that move passively downstream, while the tail-down models may be useful for modelling the composition of organisms such as macroinvertebrates and fish which have the capacity to actively move both up and downstream (Peterson et al., 2013; Isaak et al., 2014).

In addition, a spatial stream-network model may be fit using a mixed-covariance structure (mixed-model), which is based on a combination of two or more autocovariance models, including tail-up and tail-down as well as covariance structure based on Euclidean distance (Peterson and Ver Hoef, 2010). Three parameters are estimated when a single autocovariance function is fit to the data: (i) the partial sill, (ii) the nugget effect, and (iii) the range parameter. The nugget effect captures variability that occurs at a scale finer than the closest measurements (fine-scale variability as the distance between locations approaches zero), as well as measurement error (Peterson et al., 2013; Frieden et al., 2014; Isaak et al., 2014). The partial sill represents the variance of the autocorrelated process without the nugget effect, while the range describes how quickly autocorrelation decreases with distance (Peterson et al., 2013; Frieden et al., 2014; Isaak et al., 2014). In a mixed model (covariance mixture), a partial sill and range parameter are estimated for each model, as well as, an overall nugget effect, and these parameters determine the relative influence that each component will have on the mixture (Ver Hoef and Peterson, 2010). An advantage of a covariance mixture is that: (i) it produces a flexible covariance structure which simultaneously accounts for many types of spatial relationships and avoids the need to choose a specific function, (ii) the combination of the tail-up and tail-down covariance matrices allows for the possibility of more autocorrelation among flow-connected pairs of sites, with somewhat less autocorrelation among flow-unconnected pairs of sites (Peterson and Ver Hoef, 2010). It also offers a flexible approach that can be used to capture complex and multi-scale spatial patterns often found in stream datasets (Peterson and Ver Hoef, 2010; Frieden et al., 2014).

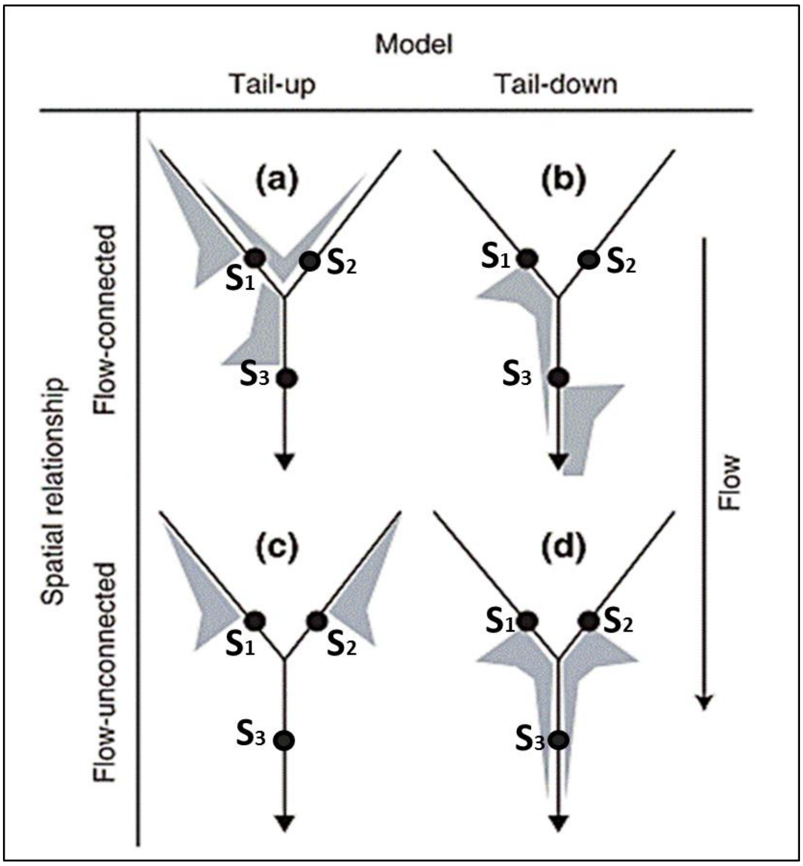

Fig.3. Flow-connected (a and b) and flow-unconnected (c and d) spatial relationships on a stream network. The tail-up (a and c) and tail-down (b and d) autocovariance models are based on moving-average (MA) functions (shown in gray) and use hydrologic distance. The MA width representing the strength of the influence for each potential neighboring location. Spatial autocorrelation occurs between locations when the MA functions overlap. Tail-down models permit correlation between flow-connected (S_1 and S_3, S_2 and S_3) and flow-unconnected locations (S_1 and S_2), while tail-up models restrict autocorrelation to flow-connected locations (S_1 and S_3, S_2 and S_3). The tail-up MA functions must be split at stream confluences using spatial weights to ensure that more influential segments receive a stronger weighting in the models (adapted from: Peterson and Ver Hoef, 2010).

2.5 Spatial-stream-network modelling: model fitting, model selection and prediction.

We used R version 3.1.2 (R Core Team, 2014) and the SSN package (Ver Hoef et al., 2014) to fit a suite of spatial stream-network models to each of the response variables. We examined maps and histograms of the data, which included continuous variables (fluoride, TN, and TP concentrations) and counts (taxon richness and TARISS). We also examined Torgegrams of the data. A Torgegram is used to display semivariance as a function of hydrologic distance separately for flow-connected and flow-unconnected sites, making them useful exploratory tools for visualizing different network-based patterns of spatial autocorrelation and can help inform the selection of candidate models for fitting (Peterson et al., 2013; Ver Hoef et al., 2014).

Spatial-stream-network models make use of a linear mixed-modelling approach to explain the variance in observations. It takes the following general form:

$$y = X\beta + z + \varepsilon \quad \ldots\ldots\ldots \quad (1)$$

where y is a vector of observations, X is a design matrix for fixed effects (variables that are measured and explain the general spatial patterns in the observations), β is a vector of coefficients for the fixed effects, z contains spatially-autocorrelated random effects (random variables with a spatial autocovariance structure modelled on the residuals of the observations after accounting for the fixed effects, that can represent both unmeasured and unknown factors influencing observations) and ε is a vector of independent random errors (Peterson and Ver Hoef, 2010; Peterson et al., 2013).

We fitted generalized linear models to the data using the *glmssn* function of the SSN package and examined the residuals using residual plots. We included five covariates (i.e., Elevation, TN=Total Nitrogen, TP=Total phosphorus, Agricultural land = Agrc.Land (percentages of agricultural land-use in the entire watershed upstream of each site), upstream distance= upDist, (the total distance from the uppermost location (upstream) on each line (stream) segment) in the taxon richness, PCoA1 and TARISS models. For the fluoride, TN, and TP models three covariates (i.e., Elevation, Agricultural land and upstream distance) were included. We used Gaussian distribution to fit the model for the fluoride, TN, and TP, and a Poisson error distribution for the TARISS, PCoA1 and Taxon richness. We used a two-step model selection procedure to evaluate the models and select the most suitable covariance structure. First, we fixed the covariance structure (a mixture of Exponential.tailup, Exponential.taildown, and Exponential.Euclid) independently for each of the response variables and selected the most important explanatory variables (covariates) using the Akaike information criterion (AIC; Akaike, 1974). Secondly, we selected the most appropriate covariance structure and spatial-weighting scheme. We fixed the selected explanatory variables and then compared every linear combination of tail-up, tail-down, and Euclidean covariance structures, where five different auto-covariance functions were tested for each model type (i.e., Exponential.tailup and Exponential.taildown, LinearSill.tailup and Mariah.taildown, Mariah.tailup, LinearSill.taildown, Spherical.tailup, Spherical.taildown, and Exponential.Euclid) with restricted maximum likelihood (REML) which is less biased than maximum likelihood (ML) (Cressie, 1993). The *InfoCritCompare* function in the SSN package was used to calculate a variety of measures of model performance, including the AIC value and root-mean- square-prediction error (RMSPE). Here the AIC can be used with REML because the fixed effects are not changing among models. The best model is the one with the smallest RMSPE and AIC, meaning that its likelihood is the highest, downweighted by its number of parameters. Bias was estimated using leave-one-out cross-validation, as implemented by the *CrossValidationStatsSSN* function of the SSN package. Once the final model was identified, we used the universal kriging algorithm (Cressie, 1993; Ver Hoef et al., 2014) to generate predictions and their variance at the prediction sites (unsampled locations) using the *predict* function of the SSN package. Predictions and their standard errors vary depending on the estimated regression coefficients and distances to observed data sites. If the explanatory variables at the prediction site are not well represented in the observed data set a large standard error will be assigned to the prediction. The predictions change gradually along stream segments and the prediction standard errors tend to be smaller near observed data and increase as a function of distance (Peterson and Ver Hoef, 2010).

Finally, a non-spatial model was fit to each of the response variables (i.e., fluoride, TN, TP, PCoA1, TARISS, and taxon richness) for comparison with the fitted spatial models. This allowed us to assess the effect of accounting spatial autocorrelation in the models.

All statistical modelling was performed in R version 3.6.3 (R Core Team, 2020) using the packages SSN, sp, RSQLite, rgeos, maps, vegan, and maptools.

3. Results

Torgegram plots for water chemistry variables (i.e., fluoride, TN, and TP) and macroinvertebrate indices (i.e., taxon richness, PCoA1 and TARISS) are presented in Fig. 4. A visual examination of Torgegrams suggested that water chemistry variables and macroinvertebrate indices exhibited both flow-connected and flow-unconnected patterns of spatial autocorrelation at different spatial scales and that fitting a mixed-covariance structure that includes both tail-up and tail-down autocorrelation models may be appropriate.

The statistics for the spatial (best models) and non-spatial models developed for the water chemistry (i.e., fluoride, TN, and TP) and macroinvertebrate indices (i.e., taxon richness, PCoA1 and TARISS) are presented in Table 1. Spatial models (with covariance mixtures that included TU and TD components) explained higher variation in water chemistry and macroinvertebrates indices ($0.232 \geq R^2 \leq 0.317$; $106.10 \geq$ AIC ≤ 205.49) compared to non-spatial model ($0.072 \geq R^2 \leq 0.158$; $136.03 \geq$ AIC ≤ 286.52). Similarly, spatial models had the smallest RMSPE values ($0.76 \geq$ RMSPE ≤ 1.97) compared to the non-spatial model ($1.21 \geq$ RMSPE ≤ 2.95) (Table 1). The results of the covariance mixtures for all five spatial models are presented in Table S1.

For the spatial models, the optimal covariance structure, based on the lowest RMSPE and AIC values, varied between water chemistry variables and macroinvertebrate indices (Table 1). The tail-up and tail-down covariance mixture had the most predictive power for all the variables. Tail-up spatial covariance captured a larger portion of water chemistry variance (varcomp ≥ 0.331) compared to tail-down spatial covariance function (varcomp $\leq$ 0.292) (Table 1). In contrast, tail-down spatial covariance captured a larger portion of macroinvertebrate indices variance (varcomp $\geq$ 0.561) compared to tail-up spatial covariance (varcomp $\leq$ 0.051). The nugget estimates produced differed between response variables. Fluoride, TN, and TP models had small nugget estimates, which included less than 8.3% of the variability in the data (Table 1). The nugget estimates for the taxon richness, PCoA1 and TARISS models were larger and represented between 9.6 % and 18.1% of the variability in the data.

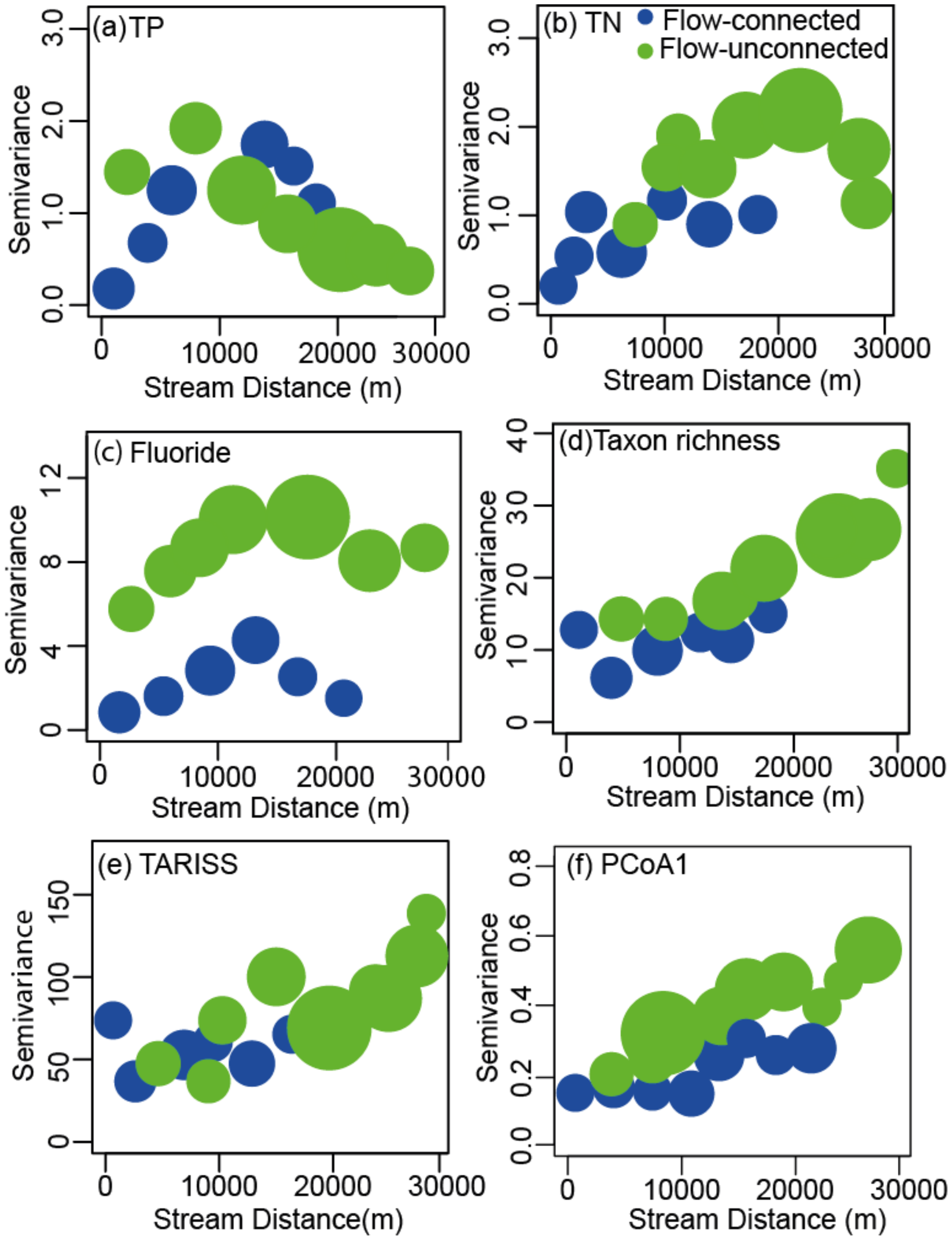

Fig.4. The Torgegram for the water chemistry variables (a, b, and c) and macroinvertebrate indices (d , e, and f) displaying semivariance as a function of hydrologic distance separately for flow-connected and flow-unconnected relationships, with the size of the circle proportional to the number or paired locations used to estimate the semivariance. TN= total nitrogen, TP= total phosphorus and taxon = taxon richness.

Table 1 Results of spatial stream network (SSN) and non-spatial (generalized linear model) model analyses showing the final set of covariates (i.e., Elevation, Agrc.Land=Agricultural land, upDist = upstream distance, TP=Total phosphorus, TN=Total Nitrogen) selected using the minimizing AIC procedure, and covariance structures for the best models retained for each response variable (i.e., Fluoride, TP=Total phosphorus, TN=Total Nitrogen, Taxon=Taxon richness, PCoA1= principal coordinates analysis (site score first axis), TARISS= Tanzania River Scoring System). The R^2 (generalised R-squared) values indicate the percentage of variation explained by covariates (of the final model), varcomp indicates the percentage of variation explained by each covariance structure within the final model mixture, nugget (the unexplained variation) accounts for the variability that occurs at a scale finer than the closest measurements, the range represents the distance after which the spatial autocorrelation becomes zero, RMSPE denoted the root mean squared prediction error (of the final model), and AIC is the Akaike Information Criterion (of the final model).

Response Variable				**Covariance parameters**				**Model performance**		
		Covariates	**P value**	**Name**	**varcomp**	**Nugget**	**Range (m)**	**RMSPE**	**R^2**	**AIC**
Fluoride	Spatial	Elevation	0.025	Spherical.tailup	0.331	0.083	15204.18	1.62	0.291	149.72
				Spherical.taildown	0.292		15158.73			
	Non-spatial	Elevation	0.043	None		0.927		2.95	0.072	168.35
TN	Spatial	Elevation	0.021	Spherical.tailup	0.538	0.001	486.96	1.41	0.317	106.10
				Spherical.taildown	0.141		810.20			
	Non-spatial	upDist	0.036	None		0.857		2.37	0.142	134.18
TP	Spatial	upDist	0.008	Mariah.tailup	0.709	0.0002	19016.36	1.06	0.232	119.70
		Agrc.Land	0.019	LinearSill.taildown	0.027		3883.95			
	Non-spatial	upDist Elevation	0.026 0.044	None		0.842		1.52	0.158	136.03
Taxon	Spatial	TP	0.008	Mariah.tailup	0.016	0.181	2561.52	0. 76	0.241	112.11
		Elevation	0.036	LinearSill.taildown	0.561		85214.74			
	Non-spatial	TP Elevation	0.027 0.041	None		0.847		1.21	0.143	148.15
TARISS	Spatial	TP	0.005	Spherical.tailup	0.051	0.053	102.87	1.97	0.284	205.49
		TN	0.021	Spherical.taildown	0.612		24925.49			
	Non-spatial	TP	0.014	None		0.873		2.53	0.106	286.52
PCoA1	Spatial	TP Elevation	0.016 0.033	Mariah.tailup LinearSill.taildown	0.038 0.539	0.135	1032.71 26648.61	0.91	0.264	156.87
	Non-spatial	Elvation	0.039	None		0.738		1.66	0.119	184.36

The covariance mixture (that include TU and TD components) captured both fine- and broad-scale patterns of spatial autocorrelation in each of the response variables, but the relative contribution of each component differed depending on the water chemistry variables and macroinvertebrate index (Table 1). For example, the TP model was dominated by broad-scale (range =19016 m) tail-up variation (varcomp = 70.9 %), suggesting that measurements at flow-connected sites were spatially correlated to some degree. The remaining residual variation in this model was captured by a fine-scale (range = 3884 m) tail-down model. In contrast, the taxon richness, PCoA1 and TARISS models were dominated by the tail-down component (varcomp: 53.9 % and 61.2% respectively). The range parameter for the taxon richness model was 85215 m, PCoA1 was 26649 m, and TARISS was 24925m indicating that measurements at both flow-connected and flow-unconnected sites were spatially correlated to some extent. Fine-scale tail-up variation dominated the TN model (range= 487 m, varcomp = 0.538) with most of its remaining variation captured by fine-scale tail-down model (range = 810 m, varcomp = 0.141).

Prediction (at un-sampled locations) maps of water chemistry and macroinvertebrate indices are presented in Fig. 5. The SSN models provided important information about the precision (standard errors) of these predictions. The standard errors were small near measurement sites and increased as the distance to a measurement site increased. Predictions of TP concentrations ranged from 0.01 to 5.57 mg/L (Fig. 5a). The lowest concentrations were predicted in upstream tributaries, whilst the highest concentrations were predicted in downstream tributaries and to the catchment outlet. Predictions of the TN concentrations ranged from 1. 5 to 3.89 mg/L (Fig. 5b). Highest concentrations were predicted from the headwater tributaries and the downstream tributaries around the confluence of Tengeru and Malala Rivers. Predicted fluoride concentration ranged between 1.2 to 9.41 mg/L (Fig. 5c). Lowest concentrations were predicted from Malala and Tengeru River tributaries, whilst the highest concentrations were predicted from the Maji ya chai and Usa River tributaries. Predicted taxon richness ranged from 1.28 to 12.51(Fig. 5d). The lowest taxon richness was predicted from the upstream tributaries, whilst the highest predictions were made around the middle-reaches and along the Usa and Maji ya Chai Rivers. The highest PCoA1 were predicted along the Usa and Tengeru Rivers. Predicted PCoA1 ranged from -0.30 to 1.20 (Fig.5e). The models provided relatively weak predictions of TARISS with high standard errors in most of the locations (Fig. 5f). Predictions of TARISS ranged from 1.6 to 105. 98. The lowest TARISS were predicted from the upstream tributaries, whilst the highest TARISS predictions were made at the middle-reaches.

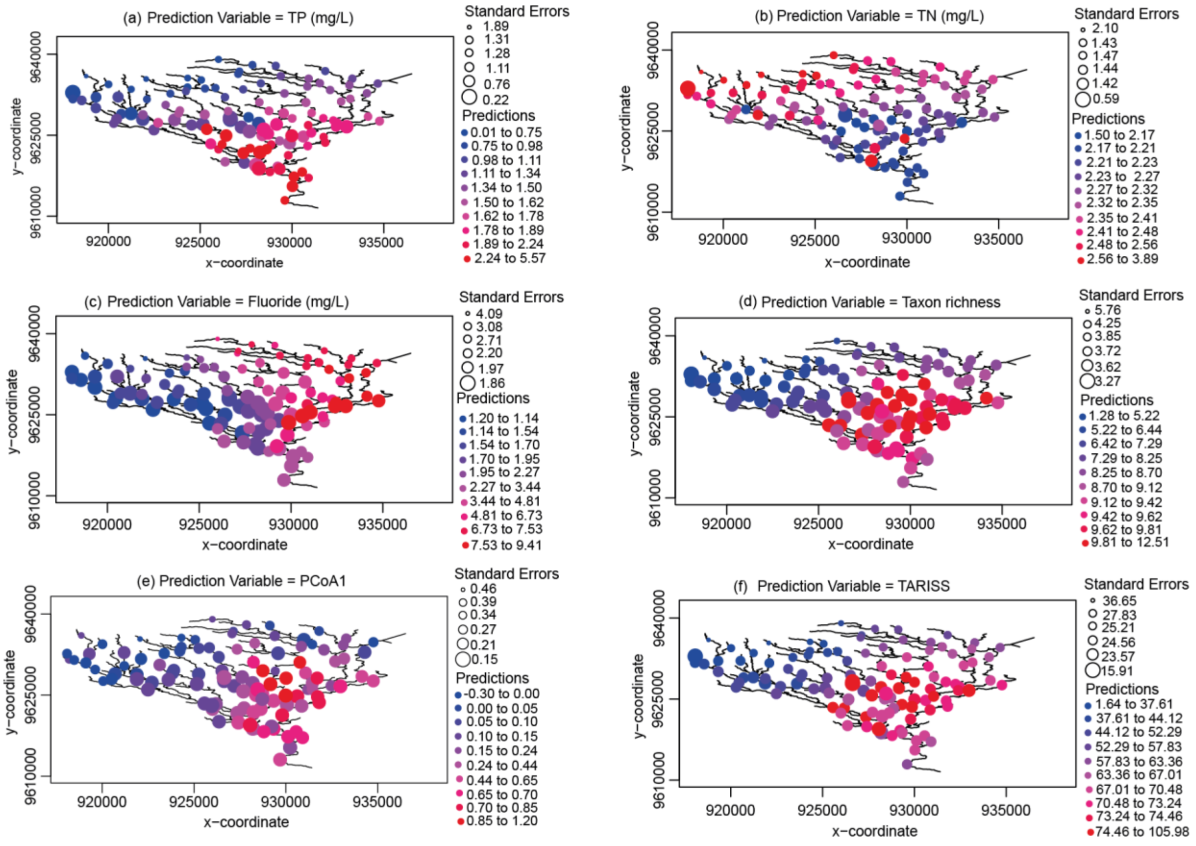

Fig. 5. Predictions of (a) total phosphorus concentrations, (b) total nitrogen concentrations, (c) fluoride concentrations, (d) taxon richness, (e) PCoA1, and (f) TARISS. Circle color represent the concentrations of water chemistry and number of taxon richness and TARISS, and circle size represent the standard error of the prediction: large circle = small standard error, small circle = large standard error (i.e., a more accurate point stands out more in the graphic). The predictions change gradually along stream segments and the prediction standard errors tend to be smaller near observed data and increase as a function of distance.

4. Discussion

We examined the role of stream network structure in determining the spatial patterns (variation and distribution) of benthic macroinvertebrate indices (i.e., taxon richness and TARISS) and water chemistry (i.e., fluoride, total nitrogen, and total phosphorus) at the catchment scale using spatial stream network (SSN) models. We used a dataset of water chemistry and benthic macroinvertebrate indices collected at forty monitoring sites in the Usa-Kikuletwa River catchment (UKRC) in northeastern Tanzania. Our results provide evidence that spatial patterns and spatial autocorrelation exist in stream water chemistry (i.e., fluoride, total nitrogen, and total phosphorus) and macroinvertebrate indices (i.e., Taxon richness and TARISS) in the UKRC, comprising both flow-connected (tail-up) and flow-unconnected (tail-down) spatial relationships. We also found that patterns of spatial autocorrelation and the spatial distance (over which variables were spatially correlated) differed between water chemistry and macroinvertebrate response variables. Yet, the spatial relationships and spatial autocorrelation were not always straightforward. The differences in spatial dependence, suggest that stream water chemistry concentrations and macroinvertebrate indices are influenced by diverse ecological and hydrological processes acting at different spatial scales. In addition, accounting for spatial autocorrelation improved models performance (high generalised R-square value (R^2), small prediction error (RMSE) and Akaike Information Criterion (AIC)) compared to non-spatial models, as often observed in other studies using stream-network models (e.g., Peterson et al., 2006; Frieden et al., 2014; Isaak et al., 2017; Neill et al., 2018; Larsen et al., 2019).

Autocorrelation among flow-connected locations is most relevant to stream water chemistry because it represents the relationship along the downstream continuum. The spatial model developed for TP indicated flow-connected spatial dependence over a broad-scale (range = 19000m), suggesting an influence of flow-accumulation on the spatial structure. This model contained upstream-distance and percentage agricultural-land as influential covariates. This is intuitive given that the unidirectional flow of water in river networks dictates that each sampling site is influenced by upstream sites, as a result, water chemistry attributes in river systems may not be spatially independent (Gardner and Mcglynn, 2009). In addition, the inclusion of agricultural land as an influential covariate in the best model suggests that leaching from agricultural areas may have a strong influence on TP concentrations in the river system and may produce a broad-scale continuous pattern along the river network (Peterson et al., 2006; Mcguire et al., 2014). Furthermore, the lowest proportion of unexplained variance (nugget = 0.0002) in the TP spatial model may indicate that the distance between the survey sites was fine enough to capture the spatial variability in TP concentrations in the catchment (Peterson et al., 2006).

TN concentrations displayed fine-scale spatial autocorrelation, whereby the range was reached at the shortest distance (range = 0.49 km), indicating patchiness or discontinuity in TN concentrations along the stream network. This may seem counterintuitive given that stream water chemistry concentrations are not likely to show strong variability (independence) over very short distances. The observed pattern may indicate that in-stream uptake of TN may be occurring over very short distances because of biological demands (including microbial denitrification, microbial immobilization, and plant uptake) (Dent and Grimm, 1999; Gardner and Mcglynn, 2009; Mcguire et al., 2014; Helton et al., 2017), suggesting strong in-stream processing influence on spatial variation over short flow-connected distances. Another plausible explanation for the fine-scale spatial autocorrelation in TN concentrations might be the influence of local-scale factors, such as point sources of pollution from nearby farms or pit-latrines (highly localized sources without a fixed spatial location) which were not included in our models, which might have introduced patchiness over short distances along the stream network (Gardner and Mcglynn, 2009; Peterson et al., 2006). A study by Elisante and Muzuka (2016) indicated that poor sanitation and domestic waste treatment services are among the major sources of nitrate pollution in surface- and ground-waters along the slopes of Mount Meru.

Fluoride showed a relatively mid- and broad scale-range spatial autocorrelation among sites that included both flow-connected and flow-unconnected relationships (range ≥15000 m). The flow-unconnected relationships may represent patterns of spatial correlation of tributary branches due to the influence of coarse-scale landscape factors, such as geology or soil type, that may have an effect on stream water chemistry concentrations rather than the longitudinal (connectivity) movement of chemicals through a stream network (Dent and Grimm, 1999; Peterson et al., 2006; Mcguire et al., 2014). Even though catchment geological characteristics were not accounted for in our models, differences in mineralogy or geological formation among sites, which have an effect on fluoride dissolution rate, have been indicated to influence the occurrence and distribution of fluoride in the study area (Chacha et al., 2018; Kitalika et al., 2018). The high fluoride concentrations in this study were recorded on the eastern side of the catchment along the tributaries of the and Maji ya Chai River and Usa River and on the western side along the upstream tributaries of Tengeru River. Similarly, an earlier study by Kitalika et al. (2018) assessing fluoride variations in rivers on the slopes of Mt. Meru (Tanzania) recorded highest fluoride levels in Maji ya Chai River in both wet and dry seasons.

The three macroinvertebrate indices displayed both fine-and broad-scale patterns of spatial autocorrelation, but to different extents. Fine-scale (103 m) spatial autocorrelation in the TARISS model suggests that localized in-stream factors such as substratum quality, nutrient and dissolved oxygen levels may have a strong influence on the TARISS scores. This is not surprising given that TARISS scores have been shown to be correlated with local habitat characteristics including nutrient concentrations and dissolved oxygen levels, among others (Kaaya et al., 2015), many of which would be expected to produce fine-scale patterns in the macroinvertebrate pollution tolerance indices (Sandin and Johnson, 2004; Soininen and Kononen, 2004; Lücke and Johnson, 2009; Frieden et al., 2014; Kaaya et al., 2015). Similarly, the best TARISS model contained nutrient concentrations (total nitrogen and total phosphorus) as influential covariates explaining TARISS variation.

The similarity of taxon composition between sites typically decreases as the distance between them increases (Soininen et al., 2007). Yet, the rate and nature of the decrease differ according to the processes driving community composition among sites, including patterns in taxon turnover and environmental features (Rouquette et al., 2013). The importance of tail-down relationships in the PCoA1 may suggest that several sites in the study area are to some degree related, shown by the relatively low taxon turnover among sites. This indicate that macroinvertebrate communities are strongly influenced by spatial processes occurring both within and outside the river network. Most likely, the broad-scale relationship results from macroinvertebrate movement, either (i) in-stream including active or passive drifting, upstream or downstream active benthic crawling, and egg dispersal (drifting on the moving water) (Lloyd et al., 2006; Bonada et al., 2012; Larsen et al., 2019), (ii) out of the water but following the water course such as aerial dispersal of adult insects, and/or (iii) with water-associated vectors (e.g., waterfowl) (Rouquette et al., 2013). Another possible explanation for the broad-scale relationship in macroinvertebrate taxa is that regional watershed characteristics operating at multiple spatial scales, such as geomorphology, may influence macroinvertebrate assemblages through their control over channel morphology and hydrologic pattern with resulting broad-scale patterns of spatial autocorrelation in the macroinvertebrate communities (Richards et al., 1997; Li et al., 2001; Townsend et al., 2003; Sandin and Johnson, 2004). Poole (2002) argued that landscape factors such as geomorphology or bedrock geology could override longitudinal gradients, so that stream communities in a given segment may be just as similar to communities far up or downstream as they are to those in neighboring stretches.

Even though species turnover can provide important insights into the processes driving species diversity at both local and regional scales (Rouquette et al., 2013), yet, patterns of taxon turnover in river systems are likely to be complex. This is because they are are affected by the spatial configuration, connectivity and directionality of the network (Grant et al., 2007; Rouquette et al., 2013), by changes in habitat associated with longitudinal changes in river character (Vannote et al., 1980), and by both current and historical disturbance at the site, and catchment land-use (Ward and Tockner, 2001). While community composition is expected to vary with increasing spatial distance (Soininen et al., 2007), the richness of communities can be similar over large distances and across a range of environmental conditions (Bonada et al., 2012; Larsen et al., 2018). This was revealed in our study whereby taxon richness displayed broad-scale (85215m) flow-unconnected relationship.

Water chemistry variables and macroinvertebrates indices displayed patterns of spatial autocorrelation mostly at the range of ≤ 25 km. This indicates that key physical, chemical and biological processes in the UKRC operate at intermediate scales (i.e., 1-100 km) (Fausch et al., 2002; Benda et al., 2004), suggesting a spatially continuous view of rivers over this scale within the DENs for better understanding of key ecological processes (Peterson et al., 2013). As such, we recommend that this should be the scales at which basin authorities and conservation agencies should observe the river-landscape (riverscape) and priorities management and conservation actions.

Even though spatial models allowed us to categorize patterns of spatial autocorrelation in water chemistry variables and macroinvertebrate indices, obtaining a full understanding of the underlying cause is not possible, because correlation does not equal causation. Spatial autocorrelation can stem from in-stream ecological processes such as nutrients retention or transformation and dispersal or competition, but may also be driven by large-scale exogenous factors including geomorphology and climatic condition (Dent and Grimm, 1999; Benda et al., 2004, Bonada et al., 2012; Gronroos et al., 2013; Frieden et al., 2014). Therefore, the spatial structure in the models likely represents complex interactions between both in-stream and landscape factors and processes operating over multiple spatial scales (Richards et al., 1997; Bonada et al., 2012; Frieden et al., 2014).

An important value in the spatial models developed in this study was making semi-continuous catchment-wide predictions of water chemistry concentrations and macroinvertebrate indices at un-sampled locations across the stream network. The models provided good predictions for TP and fluoride concentrations in the Usa-Kikuletwa River catchment. Standard errors were smallest for predictions made at prediction sites near to sampling sites to which they were flow-connected and greatest for predictions made along tributaries that did not contain a sampling site. The model predicted high TP concentrations in the middle reaches throughout to the catchment outlet (Fig. 5a). This is not surprising given that anthropogenic activities in the catchment, particularly agricultural activities which directly influence the nutrient concentrations in the river systems, have been found to intensify in the middle and lower reaches of the catchment (Msigwa et al., 2019; Mwaijengo et al., 2020).

The spatial model predicted high fluoride concentrations along the Maji ya chai and Usa River tributaries and decreased downstream along the mainstem after the confluence with Tengeru (Fig. 5c). An interpretation of this could be that elevated concentrations along Maji ya Chai and Usa Rivers are likely diluted by downstream inputs of water, in particular from the tributary joining the mainstem. This is an advantage of using the SSN models whereby it allows stream network interactions to be inferred, due to the inclusion of a spatial autocovariance function (Ver Hoef et al., 2006). The observed trend in fluoride concentrations is confirmed in previous studies examining the distribution of fluoride concentrations on the slopes of Mount Meru which recorded high fluoride concentrations along the Maji ya chai River attributing to its basalt aquifer lithology (characterized by high fluoride levels) (Kitalika et al., 2018). These results support the increasing body of evidence suggesting that spatial models, particularly SSN models, are useful for up-scaling site-based measurements collected on river networks to provide a more continuous perspective of river characteristics (Cressie et al., 2006; Peterson and Ver Hoef, 2010, Frieden et al., 2014; Isaak et al., 2014; Neill et al., 2018).

However, the spatial model predicted higher TN concentrations in the upstream sites compared to the middle and lower reaches sites (Fig. 5b). This may seem counterintuitive given that watershed conditions at these sites were not the source of elevated TN predictions: upstream sites are relatively more pristine (less anthropogenic activities) compared to downstream sites (Msigwa et al., 2019; Mwaijengo et al., 2020). Spatial (SSN) models draw upon known observed values at neighboring correlated locations in order to improve predictions at un-sampled locations (Cressie, 1993; Ver Hoef and Peterson, 2010). When a spatial neighborhood is deficient or absent for a specific site, the SSN provides a broad-scale mean in the data but does not provide additional predictive ability at that site (Peterson and Urquhart, 2006; Garreta et al., 2010; Ver Hoef and Peterson, 2010). In this study, there were two upstream sites with high TN concentrations along the Malala and Tengeru River networks, which the SSN model may have used to predict high TN concentrations along all upstream tributaries. This is confirmed with relatively large standard errors associated with these predictions (Fig. 5b). The high predictions standard errors (uncertainty) provided by SSN model could be used to help highlight where additional monitoring could usefully take place (Peterson and Urquhart, 2006)

The spatial stream-network model predicted low taxon richness in headwater tributaries and increased along the river course in the middle-reaches sites (Fig. 5 d). The observed pattern lends support from earlier studies examining the longitudinal changes in the taxonomic richness of aquatic macroinvertebrates in river systems. In the River Continuum Concept (RCC), Vannote et al. (1980) predicted that species richness increases with stream size and reaches a maximum in mid-order streams. Similarly, Arscott et al. (2005) in their study investigating the relationship between species richness and stream size (from second- to eighth-order) in the Tagliamento River in northeastern Italy, they found low richness in headwater streams, an increase in mid-order streams and a decrease in richness in high-order streams. Furthermore, Clarke et al. (2008) in their review addressing macroinvertebrate diversity in headwater streams among different regions indicated that taxon richness of macroinvertebrates generally tends to be low in headwater streams.

Even though the spatial stream-network models accounted for spatial structure and autocorrelation in water chemistry variables and macroinvertebrate indices, the distribution of the sampling sites and the sampling design may still have got an impact on the SNN model results. The relatively small (<50) data set of spatially sparse sampling sites in this study may have contributed to the relatively low performance of the models ($R^2 \leq 0.32$). SSN models tend to perform much better with large (≥ 50 sites) and spatially dense datasets. In contrast, with a small and spatially sparse data set, network connectivity effects become weak or difficult to estimate (Isaak et al., 2014). Cressie (1993) and Ver Hoef and Peterson (2010) have specified that spatial models tend to perform better when they can ‘borrow strength’ from spatially correlated neighboring sites. For prediction sites that were distant from a flow-connected monitoring site or along a tributary with no monitoring site may have impacted SSN model predictions and their certainty. Actually, upstream sites/locations were underrepresented in the observed data, as such the accuracy of model predictions would have benefitted from additional monitoring sites located in the upstream tributaries.

Overall, water chemistry variables and macroinvertebrate indices in the UKRC exhibited patterns of spatial autocorrelation over different spatial scales including both flow-connected and flow-unconnected relationships, and that different ecological processes acting at multiple spatial scales account for the observed spatial patterns. More importantly, this study adds to current research signifying the importance of explicitly accounting for spatial configuration of stream networks (i.e., dendritic network structure) and spatial autocorrelation when modelling physical, chemical and biological processes across stream networks (Peterson et al., 2013; Isaak et al., 2014; Mcguire et al., 2014), and the value of geostatistical tools, particularly SSN, to undertake such modelling (Peterson et al., 2013; Ver Hoef and Peterson, 2010; Isaak et al., 2014; Ver Hoef et al., 2014). Finally, a spatial stream network model could be used to support river basin management in the region: inferences about regional river conditions can be generated and thus can be used to locate potentially impaired river segments in a rapid and cost-efficient manner.

References

Akaike, H., 1974. A New Look at the Statistical Model Identification. IEEE Trans. Automat. Contr. AC-19, 716–723.

APHA, 2012. Stand Methods for Examination of Water and Waste water, 22nd ed. ed. American Public Health Association,American Water Works Association,Water Environmental Federation, Washington, DC.

Arscott, D.B., Tockner, K., Ward, J. V, 2005. Lateral organization of aquatic invertebrates along a corridor of a braided floodplain river. J. North Am. Benthol. Soc. 24, 934–954.

Benda, L., 2008. Confluence environments at the scale of river networks, in: River Confluences, Tributaries and the Fluvial Network, Rice SP, RoyAG, Rhoads BL (eds). JohnWiley & Sons: Chichester, UK. pp. 271–300.

Benda, L., Poff, L.N., Miller, D., Dunne, T., Reeves, G., Pess, G., Pollock, M., 2004. The Network Dynamics Hypothesis : How Channel Networks Structure Riverine Habitats. Bioscience 54, 413–427.

Bernhardt, E.S., Likens, G.E., Buso, D.C., Driscoll, C.T., 2003. In-stream uptake dampens effects of major forest. Proc. Natl. Acad. Sci. 100, 10304–10308.

Bonada, N., Doledec, S., Statzner, B., 2012. Spatial autocorrelation patterns of stream invertebrates : exogenous and endogenous factors. J. Biogeogr. 39, 56–68.

Brown, B.L., Swan, C.M., 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. J. Anim. Ecol. 79, 571–580.

Chacha, N., Njau, K.N., Lugomela, G. V, Muzuka, A.N.N., 2018. Hydrogeochemical characteristics and spatial distribution of groundwater quality in Arusha well fields , Northern Tanzania. Appl. Water Sci. 8, 1–23.

Clarke, A., Nally, R.M., Bond, N., Lake, P.S., 2008. Macroinvertebrate diversity in headwater streams : a review. Freshw. Biol. 53, 1707–1721.

Cressie, N., Frey, J., Harch, B., Smith, M., 2006. Spatial Prediction on a River Network. J. od Agric. Biol. Environ. Stat. 11, 127–150.

Cressie, N.A.., 1993. Statistics for Spatial Data (revised edition). Wiley, New York, USA.

Croft, P.S., 1986. A Key to the Major Groups of British Freshwater Invertebrates. Rep. Pub. FSC. 1986.

Davies, B., Day, J., 1998. Vanishing Waters: Keys to common macroinvertebrate taxa of South African Inland Waters.

Dent, L.C., Grimm, N.B., 1999. Spatial Heterogeneity of Stream Water Nutrient Concentrations Over Successional Time. Ecology 80, 2283–2298.

Elisante, E., Muzuka, A.N.N., 2016. Assessment of sources and transformation of nitrate in groundwater on the slopes of Mount Meru , Tanzania. Environ. Earth Sci. 75, 1–15.

Fagan, W.F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83, 3243–3249.

Fausch, K.D., Torgersen, C.E., Baxter, C. V, Li, H.W., 2002. Landscapes to Riverscapes : Bridging the Gap between Research and Conservation of Stream Fishes. Bioscience 52, 483–498.

Frieden, J.C., Peterson, E.E., Webb, J.A., Negus, P.M., 2014. Improving the predictive power of spatial statistical models of stream macroinvertebrates using weighted autocovariance functions. Environ. Model. Softw. 60, 320–330.

Ganio, L.M., Torgersen, C.E., Gresswell, R.E., 2005. A geostatistical approach for describing spatial pattern in stream networks. Front. Ecol. Environ. 3, 138–144.

Gardner, K.K., Mcglynn, B.L., 2009. Seasonality in spatial variability and influence of land use / land cover and watershed characteristics on stream water nitrate concentrations in a developing watershed in the Rocky Mountain West. Water Resorces Res. Res. 45, 1–14.

Gerber, A., Gabriel, M.J.M., 2002. Aquatic Invertebrates of South African Rivers: Field Guide. Institute for Water Quality Studies.

Grant, E.H.C., Green, L.E., Lowe, W.H., 2009. Salamander occupancy in headwater stream networks. Freshw. Biol. 54, 1370–1378.

Grant, E.H.C., Lowe, W.H., Fagan, W.F., 2007. Living in the branches : population dynamics and ecological processes in dendritic networks. Ecol. Lett. 10, 165–175.

Isaak, D.J., Hoef, J.M. Ver, Peterson, E.E., Horan, D.L., Nagel, D.E., 2017. Scalable population estimates using spatial-stream-network (SSN) models , fish density surveys , and national geospatial database frameworks for streams. Can. J. Fish. Aquat. Sci. 74, 147–156.

Isaak, D.J., Peterson, E.E., VerHoef, J.M., Wenger, S.J., Falke, J.A., Torgersen, C.E., Sowder, C., Steel, A.E., Fortin, M., Jordan, C.E., Ruesch, A.S., Som, N., Monestiez, P., 2014. Applications of spatial statistical network models to stream data. WIREs Water 1, 277–294.

Jackson, F.L., Fryer, R.J., Hannah, D.M., Millar, C.P., Malcolm, I.A., 2018. A spatio-temporal statistical model of maximum daily river temperatures to inform the management of Scotland ' s Atlantic salmon rivers under climate change. Sci. Total Environ. 612, 1543–1558.

Jones, L.A., Muhlfeld, C.C., Marshall, L.A., Mcglynn, B.L., Kershner, J.L., 2014. Estimating Thermal Regimes of Bull Trout and Assessing the Potential Effects of Climate Warming on Critical Habitats. River Res. Appl. 30, 204–216.

Kaaya, L.T., Day, J.A., Dallas, H.F., 2015. Tanzania River Scoring System (TARISS): a macroinvertebrate-based biotic index for rapid bioassessment of rivers. African J. Aquat. Sci. 40, 109–117.

Kiptala, J.K., Mohamed, Y., Mul, M.L., Cheema, M.J.M., Van Der Zaag, P., 2013. Land use and land cover classification using phenological variability from MODIS vegetation in the Upper Pangani River Basin , Eastern Africa. Phys. Chem. Earth 66, 112–122.

Kiptala, J.K., Mul, M.L., Mohamed, Y., Zaag, P. van der, 2013. Modelling stream flow and quantifying blue water using modified STREAM model in the Upper Pangani River Basin , Eastern Africa. Hydrol. Earth Syst. Sci. 10, 15771–15809.

Kitalika, A.J., Machunda, R.L., Komakech, H.C., Njau, K.N., 2018. Fluoride Variations in Rivers on the Slopes of Mount Meru in Tanzania. Hindawi 1–18.

Koenig, W.D., 1999. Spatial autocorrelation of ecological phenomena. Trends Ecol. Evol. 14, 22–26.

Kuemmerlen, M., Reichert, P., Siber, R., Schuwirth, N., 2019. Ecological assessment of river networks : From reach to catchment scale. Sci. Total Environ. 650, 1613–1627.

Larsen, S., Bruno, M.C., Vaughan, I.P., Zolezzi, G., 2019. Testing the River Continuum Concept with geostatistical stream-network models. Ecol. Complex. 39, 1–12.

Larsen, S., Chase, J.M., Durance, I., Ormerod, S., 2018. Lifting the veil : richness measurements fail to detect systematic biodiversity change over three decades. Ecology 99, 1316–1326.

Legendre, P., 1993. Spatial Autocorrelation : Trouble or New Paradigm ? Ecology 74, 1659–1673.

Li, J., Herlihy, A., Gerth, W., Kaufmann, P., Gregory, S., Urquhart, S., Larsen, D.P., 2001. Variability in stream macroinvertebrates at multiple spatial scales. Freshw. Biol. 46, 87–97.

Lücke, J.D., Johnson, R.K., 2009. Detection of ecological change in stream macroinvertebrate assemblages using single metric, multimetric or multivariate approaches. Ecol. Indic. 9, 659–669.

Mcguire, K.J., Torgersen, C.E., Likens, G.E., Buso, D.C., Lowe, W.H., Bailey, S.W., 2014. Network analysis reveals multiscale controls on streamwater chemistry. Proc. Natl. Acad. Sci. U.S.A. 1–6.

Meru District Council, 2013. Meru district council profile.Arusha, Tanzania. p80 (unpublished report).

Msigwa, A., Komakech, H.C., Verbeiren, B., Salvadore, E., Hessels, T., Weerasinghe, I., Griensven, A. van, 2019. Accounting for Seasonal Land Use Dynamics to Improve Estimation of Agricultural Irrigation WaterWithdrawals. Water 11, 1–20.

Mwaijengo, G.N., Msigwa, A., Nicholas, K., Brendonck, L., Vanschoenwinkel, B., 2020. Where does land use matter most ? Contrasting land use effects on river quality at different spatial scales. Sci. Total Environ. 715, 1–14.

National Sample Census of Agriculture(NSCA), 2007. United Republic of Tanzania, Regional Report: Arusha Region: Volume Vb.

Neill, A.J., Tetzlaff, D., Strachan, N.C.J., Hough, R.L., Avery, L.M., Watson, H., Soulsby, C., 2018. Using spatial-stream-network models and long-term data to understand and predict dynamics of faecal contamination in a mixed land-use catchment. Sci. Total Environ. 612, 840–852.

PBWO/IUCN, 2007. Pangani River System: State of the Basin Report 2007.Moshi, Tanzania.

Peterson, E.E., Merton, A.A., Theobald, D.M., Urquhart, N.S., 2006. Patterns of Spatial Autocorrelation in Stream Water Chemistry. Environ. Monit. Assess. 121, 571–596.

Peterson, E.E., Urquhart, N.S., 2006. Predicting Water Quality Impaired Stream Segments using Landscape-Scale Data and a Regional Geostatistical Model: A Case Study in Maryland. Environ. Monit. Assess. 121, 615–638.

Peterson, E.E., Ver Hoef, J.M., 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks. Ecology 91, 644–651.

Peterson, E.E., Ver Hoef, J.M., 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks. Ecology 91, 644–651.

Peterson, E.E., Ver Hoef, J.M., Isaak, D.J., Falke, J.A., Fortin, M.-J., Jordan, C.E., McNyset, K., Monestiez, P., Ruesch, A.S., Sengupta, A., Som, N., Steel, A., Theobald, D.M., Torgersen, C.E., Wenger, S.J., 2013. Modelling dendritic ecological networks in space : an integrated network perspective. Ecol. Lett. 16, 707–719.

Peterson, E.E., VerHoef, J.M., 2014. STARS : An ArcGIS Toolset Used to Calculate the Statistical Models to Stream Network Data. J. Stat. Softw. January 56, 1–17.

Poole, G.C., 2002. Fluvial landscape ecology : addressing uniqueness within the river discontinuum. Freshw. Biol. 47, 641–660.

R Core Team, ., 2014. R: a language and environment for statistical computing [WWW Document]. URL http://www.R- project.org/.

Richards, C., Haro, R.J., Johnson, L.B., Host, G.E., 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. Biol. 37, 219–230.

Sandin, L., Johnson, R.K., 2004. Local , landscape and regional factors structuring benthic macroinvertebrate assemblages in Swedish streams. Landsc. Ecol. 19, 501–514.

Scown, M.W., Mcmanus, M.G., Carson, J.H., Nietch, C.T., 2017. Improving Predictive Models of In-Stream Phosphorus Concentration Based on Nationally-Available Spatial Data Coverages. J. Am. Water Resour. Assoc. 45840, 1–17.

Selemani, J.R., Zhang, J., Muzuka, A.N.N., Njau, K.N., Zhang, G., Maggid, A., Mzuza, M.K., Jin, J., Pradhan, S., 2017. Seasonal water chemistry variability in the Pangani River basin , Tanzania. Environ. Sci. Pollut. Res. 24, 26092–26110.

Seymour, M., Fronhofer, E.A., Altermatt, F., 2015. Dendritic network structure and dispersal affect temporal dynamics of diversity and species persistence. Oecologia 908–916.

Soininen, J., Kononen, K., 2004. Comparative study of monitoring South-Finnish rivers and streams using macroinvertebrate and benthic diatom community structure. Aquat. Ecol. 38, 63–75.

Soininen, J., Mcdonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. Ecography (Cop.). 30, 3–12.

Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region. Econ. Geogr. 46, 234–240.

Vannote, R.L., Minshall, G.W., Cummins, K., Sedell, J.R., 1980. The River Continuum Concept. Can J Fish Aquat Sci 37, 130–7.

Ver Hoef, J.M., Peterson, E., Theobald, D., 2006. Spatial statistical models that use flow and stream distance. Environ.Ecol.Stat 13, 449–464.

Ver Hoef, J.M., Peterson, E.E., 2010. A Moving Average Approach for Spatial Statistical Models of Stream Networks. J. Am. Stat. Assoc. 105, 1–18.

Ver Hoef, J.M., Peterson, E.E., Clifford, D., Shah, R., 2014. SSN : An R Package for Spatial Statistical Modeling on Stream Networks. J. Stat. Softw. 56, 1–49.

VerHoef, J.M., Peterson, E.E., 2012. A Moving Average Approach for Spatial Statistical Models of Stream Networks A Moving Average Approach for Spatial Statistical. J. Am. Stat. Assoc. 105, 6–18.

Supplementary Information to Chapter 3

Table S1 Results of spatial stream network (SSN) showing the covariance structures for several different spatial models. The R^2 (generalised R-squared) values indicate the percentage of variation explained by covariates, RMSPE denoted the root mean squared prediction error, and AIC is the Akaike Information Criterion.

Response Variable	Covariance parameters	Model performance		
		RMSPE	R^2	AIC
Fluoride	Exponential.tailup+ Exponential.taildown	1.79	0.203	150.96
	LinearSill.tailup + Mariah.taildown	1.84	0.198	152.01
	Mariah.tailup + LinearSill.taildown	1.73	0.214	150.64
	Spherical.tailup + Spherical.taildown	1.62	0.291	149.72
	Exponential.Euclid	1.95	0.179	154.85
TN	Exponential.tailup+ Exponential.taildown	1.51	0.251	129.61
	LinearSill.tailup + Mariah.taildown	1.47	0.259	126.82
	Mariah.tailup + LinearSill.taildown	1.43	0.278	116.47
	Spherical.tailup + Spherical.taildown	1.41	0.317	106.10
	Exponential.Euclid	1.59	0.210	131.32
TP	Exponential.tailup+ Exponential.taildown	1.12	0.199	120.58
	LinearSill.tailup + Mariah.taildown	1.18	0.184	121.37
	Mariah.tailup + LinearSill.taildown	1.06	0.232	119.70
	Spherical.tailup + Spherical.taildown	1.27	0.182	121.81
	Exponential.Euclid	1.34	0.179	123.66
Taxon	Exponential.tailup+ Exponential.taildown	0.91	0.183	123.35
	LinearSill.tailup + Mariah.taildown	0.82	0.207	119.63
	Mariah.tailup + LinearSill.taildown	0.76	0.241	112.11
	Spherical.tailup + Spherical.taildown	0.88	0.194	120.49
	Exponential.Euclid	0.95	0.161	129.15
TARISS	Exponential.tailup+ Exponential.taildown	2.09	2.562	215.67
	LinearSill.tailup + Mariah.taildown	2.13	0.183	219.19
	Mariah.tailup + LinearSill.taildown	2.28	0.179	224.38
	Spherical.tailup + Spherical.taildown	1.97	0.284	205.49
	Exponential.Euclid	2.34	0.159	246.72
PCoA1	Exponential.tailup+ Exponential.taildown	1.38	0.173	171.23
	LinearSill.tailup + Mariah.taildown	1.05	0.218	160.41
	Mariah.tailup + LinearSill.taildown	0.91	0.264	156.87
	Spherical.tailup + Spherical.taildown	1.12	0.197	164.56
	Exponential.Euclid	1.46	0.165	176.23

Table S2 The eigenvalues for the first three PCoA axes (showing variation in macroinvertebrate communities) for each site in the Usa-Kikuletwa River.

Site	PCoA1	PCoA2	PCoA3
N2	0.2831	0.2653	0.0524
N3	0.5856	-0.0937	0.0053
N4	0.5084	0.3172	0.2166
N5L	-0.0618	-0.1358	0.1773
N5R	0.6913	0.2518	-0.0546
N6L	0.2432	-0.0245	0.0949
N6R	0.0387	0.2867	0.0284
N8	0.7114	0.1543	0.1085
N9	0.0471	0.0955	-0.1398
N10R	0.3916	0.1716	-0.0626
N10C	-0.0698	0.2549	0.0034
N12L	0.2873	-0.1571	-0.0259
N12R	0.0117	0.0054	0.0795
N13	-0.1599	0.0904	-0.2263
N14L	0.0325	0.0337	-0.0076
N14R	-0.1231	0.0581	-0.2392
N15	0.1953	0.0013	0.0019
N16	0.4064	0.1062	0.3043
N18	0.0522	-0.0193	0.0086
N19	-0.2165	0.1246	0.0971
N20	0.5918	0.0123	-0.0207
N21	0.6053	-0.0255	0.0532
N22	0.0082	0.0729	0.0238
N23	-0.0588	-0.1395	0.0016
N24	0.6829	0.0206	0.1335
N25U	0.0831	-0.0654	0.0174
N25D	0.4176	-0.0415	0.0086
N28	0.4081	0.2733	-0.0094
N31	0.0784	0.4891	-0.1436
N32	0.6275	-0.0584	-0.0127
N33	0.4087	0.0027	0.0452
N34	0.3122	-0.2234	0.1449
N36	-0.1963	0.3015	-0.1212
N37	-0.0018	0.1186	0.0045
N38	0.0528	0.0528	0.0012
N39	0.1788	-0.1483	0.0466
N40L	0.1816	0.1594	0.1754
N40R	0.3313	0.0316	0.0049
N41	-0.0125	0.1978	-0.0631
N42	0.1369	-0.1728	0.0211

Chapter 4

Seasonal river connections modulate community structure in tropical temporary pools

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Abstract

In natural river systems in arid and semi-arid lands, surrounding floodplains may contain temporary pools. Some of these may be mainly rain-filled (endorheic systems) while others may be partly rain-fed but connect to the flooding river during a good rainy season (river connected pools). However, how seasonal river flooding affects the community characteristics in temporary floodplain pools is not well understood. Here, we studied the role of seasonal river connections in modulating macroinvertebrate community structure in a set of temporary pools in a river-floodplain ecosystem in northeastern Tanzania. We compared macroinvertebrate communities of a set of endorheic versus river connected pools. We also assessed the relative importance of hydrological connectivity and habitat heterogeneity as drivers of community structure between habitat types. Macroinvertebrate communities from the two habitats were clearly differentiated. Spatial species turnover (β-diversity) was higher in river connected pools, but endorheic ones supported a higher taxon richness (alpha diversity). Macroinvertebrate community dissimilarity between pools was largely determined by turnover, rather than by nestedness. Hydrological connectivity was positively associated with electric conductivity and negatively with nutrient concentrations in the river connected pools. In addition, the river facilitated fish dispersal which likely excluded predation sensitive taxa such as the large branchiopod crustaceans *Streptocephalus bourquinii*, *Streptocephalus wirminghausi*. Indicator species analysis revealed no specific fauna unique to river connected pools. This study illustrates that land management schemes that aim to preserve temporary pool biodiversity should strive to include both endorheic and river connected pools to support high regional biodiversity, potentially with a priority for the more diverse endorheic systems.

Keywords: temporary pools, macroinvertebrates, hydrological connectivity, endorheic pools, river connected pools, β-diversity, Ruvu River catchment

1. Introduction

Temporary pools are defined as wetlands that are generally small (< 10 ha in area) and shallow (often < 30 cm) with alternating phases of flooding and drying, and a largely autonomous hydrology (Ramsar, 2002). They typically occupy endorheic (i.e., closed hydrologic systems with no outflow) depressions, that remain filled for a sufficiently long period to allow for the development of hydromorphic soil, aquatic and semi-aquatic vegetation and specific faunal communities (Ramsar, 2002; Williams, 2006). Temporary pools occur in most climatic regions but they are most abundant in arid and semi-arid areas (Williams, 1996; Brendonck and Williams, 2000; Rhazi et al., 2001; Nhiwatiwa et al., 2017) where they are an important source of water for agricultural, wildlife and household use (Scoones, 1991; Rhazi et al., 2012; Madihi et al., 2017). They also play important roles in the landscape such as for flood control, recycling of nutrients, groundwater recharge, and removal of toxicants (Williams, 2006).

Despite their relatively small size, temporary pools, contribute significantly to local and regional biodiversity, as they can harbor taxa that are uncommon or absent in permanent aquatic habitats (Williams et al., 2003; Nicolet et al., 2004; De Meester et al., 2005; Aguilar-Alberola and Mesquita-Joanes, 2011). Unique fauna comprises various large branchiopod crustaceans such as fairy shrimp, clam shrimp, and tadpole shrimp, annual fish such as *Nothobranchius* spp., and specialist plants such as the aquatic fern *Isoetes* (Williams, 2006). In addition, they provide breeding habitats for many threatened amphibians worldwide (Kenneth and Cade, 1998; Williams, 2006). Besides their high inherent conservation value, temporary pools have also served as model systems to test ecological and evolutionary theory (De Meester et al., 2005; Vanschoenwinkel et al., 2007; Pinceel et al., 2017). However, due to their temporary nature and relatively small size and shallow depth, temporary pools are vulnerable to anthropogenic impacts, including pollution, introduction of exotic species, drainage, and land-use change (Nicolet et al., 2004; Rhazi et al., 2012; Van Den Broeck et al., 2015; Nhiwatiwa and Dalu, 2016; Madihi et al., 2017). Consequently, temporary pools are rapidly disappearing around the world (Rhazi et al., 2012; Van Den Broeck et al., 2015; Javornik and Collinge, 2016; Calhoun et al., 2017), with a global loss of over 50% during the last century (Finlayson and D’Cruz, 2005; Millennium Ecosystem Assessment, 2005; Rhazi et al., 2012). Additionally, climate change is expected to have a strong impact on these small freshwater systems (Pyke, 2005; Rosset et al., 2010; Tuytens et al., 2014). However, in most parts of the world temporary pools are not monitored and any changes in their quality and abundance remain unnoticed. This is mainly because temporary small waterbodies often lack recognition by policy and decision-makers which hinder effective conservation and sustainable management measures (Oertli et al., 2005; Turner et al., 2010): their economic value and services they provide to humanity are often underestimated and not integrated into decision making processes. In addition, there is a gap of scientific knowledge on temporary pools (Van Den Broeck, 2016), despite an increase of research and scientific publications in recent years (Oertli et al., 2009; Boix et al., 2012; Bagella et al., 2016). (Bagella et al., 2016; Boix et al., 2012).

Connectivity and isolation are principal concepts in ecology determining the distribution of organisms (Moilanen and Nieminen, 2002; Gallardo et al., 2014). Connectivity facilitates dispersal of organisms among habitat patches, increasing the resilience of ecosystems to disturbances, and supports key ecosystem processes, such as nutrient cycling (Leibold et al., 2004; Vanschoenwinkel et al., 2007; Bouviere et al., 2009; Akasaka and Takamura, 2012; Gallardo et al., 2014). Theoretical models show that increased connectivity among habitat patches can homogenize species composition among localities, decreasing community dissimilarity (β-diversity) (Chase and Ryberg, 2004; Thomaz et al., 2007). In river systems, the surrounding floodplain may comprise a mosaic of different temporary pools. They include isolated endorheic pools that are only rain-filled, and floodplain pools that besides being partly rain-filled also seasonally connect to the river channel during high flows (Ward and Stanford, 1995; Amoros and Bornette, 2002; Gallardo et al., 2014). This is described by the flood pulse concept (FPC) which promulgates the view that rivers and the fringing floodplains are integrated components of a single dynamic system, linked by strong interactions between hydrological and ecological processes (Junk et al., 1989). Contrasts in hydrological connectivity between endorheic and floodplain pools and among floodplain pools, result in a high diversity of pool habitat conditions yielding differences in community composition (Tockner et al., 1999b; Amoros and Bornette, 2002; Gallardo et al., 2014; Dube et al., 2019). As a consequence, seasonal river connections play a central role in structuring community patterns in floodplain ecosystems (Tockner et al., 1999b; Paillex et al., 2007).

Major habitat components that vary with seasonal river connectivity and directly influence biodiversity patterns in temporary pools in floodplain ecosystems include turbidity, nutrient concentrations, organic matter content and presence of fish (Tockner et al., 1999a; Amoros and Bornette, 2002). The FPC predicts that the nutrient status of the floodplain water bodies depends on the amount and quality of suspended and dissolved solids of the parent river (Junk et al., 1989). Yet, it includes the premise that internal processes of the floodplain and nutrient transfer mechanisms between the terrestrial and the aquatic phase strongly influence nutrient cycles, primary and secondary production and organic matter decomposition (Junk and Wantzen, 2004). Turbidity and dissolved nutrient concentrations of floodplain pools generally increase with connectivity to the river, which provides the pools with sediment and nutrient-rich water (Junk et al., 1989; Tockner et al., 1999a; Thomaz et al., 2007; Weilhoefer and Pan, 2008), while in disconnected (endorheic) pools, nutrient content mostly depends on successional stage and the surrounding land-use (Bornette et al., 1998; Tockner et al.,1999a). Pools that episodically connect to the river channel are likely to contain lower organic matter content, as a result of river backflow (Tockner et al., 1999a; Amoros and Bornette, 2002). In addition, fish can invade the floodplain pools during flooding events and eliminate vulnerable invertebrate species (Nhiwatiwa et al., 2009; Dube et al., 2019). In contrast, isolated endorheic pools are normally fishless, and the top predators are usually invertebrates (Spencer et al., 1999; Brendonck et al., 2002; Waterkeyn et al., 2016).

Although several authors have documented the effect of hydrological connectivity on the structure and functioning of floodplain wetlands in multiple climates (e.g., Klement Tockner et al., 1999b; Amoros and Bornette, 2002; Sheldon et., 2002; Thomaz et al., 2007; Gallardo et al., 2008; Dube et al., 2019), the mechanisms by which seasonal river connections modulate macroinvertebrate community structure in a mosaic of temporary pools in floodplain ecosystems are still not well understood (Thomaz et al., 2007). The studies suggest that macroinvertebrate patterns across hydrological gradients are complex and depend on many interrelated factors (Gallardo et al., 2014). For example, in subtropical and temperate regions, increased hydrological connectivity between the river and associated floodplain wetlands reduces macroinvertebrate species diversity by reducing spatial habitat heterogeneity (Amoros and Bornette, 2002; Gallardo et al., 2014). In contrast, Sheldon et al. (2002) found similarity in macroinvertebrate assemblages between low and high connected floodplain habitats in a semi-arid region. To resolve such conflicts and to generate more general concepts, additional knowledge is clearly required on the effects of seasonal river connections on macroinvertebrate community composition in temporary pool habitats of river-floodplain systems, and this from different regions.

The floodplain ecosystem in the Ruvu River catchment, northeastern Tanzania is an ideal system to study the effects of seasonal river flooding on the community structure of aquatic macroinvertebrates. This can be achieved by comparing macroinvertebrate communities in pools that seasonally connect to the swelling river during the high flows (i.e., river connected pools) with those from pools that lack such connection (i.e., isolated endorheic pools). A better understanding of the mechanisms by which seasonal river connections effects diversity and community structure of macroinvertebrates in floodplain habitats will help in the execution of appropriate biodiversity conservation and management actions in the region.

In the present study, we assessed the role of seasonal river connections in modulating macroinvertebrate community structure in a set of temporary pools in the Ruvu River Catchment in northeastern Tanzania. Specifically, we aimed (i) to determine the differences in environmental conditions and macroinvertebrate diversity and community composition between endorheic and river connected pools. We also aimed (ii) to identify macroinvertebrate indicator taxa for the different habitat types (i.e., endorheic versus river connected pools), and (iii) to uncover the key environmental factors that predominately influence variation in diversity and community composition of macroinvertebrates in the studied habitat types. First, we hypothesized that seasonal river connections would increase nutrient load and turbidity in the river connected pools. Second, we expected that river connections would regularly transport fish in the river connected pools which can exclude predation sensitive taxa. Third, given these contrasting conditions, we expected that different macroinvertebrate taxa might be useful as indicator species in endorheic compared to river connected pools. Fourth, we predicted that variation in community composition between habitat types will strongly reflect differences in habitat characteristics.

Finally, given that floodplain pools occur along a gradient of lateral hydrological connectivity, with related expected differences in environmental conditions and dispersal mode of organisms, we predicted that beta (β) diversity will be higher in the river connected than in the endorheic pools.

2. Materials and Methods

2.1. Study area

This study was conducted in the Ruvu River catchment located along 36.3° and 38.1° E Longitude and 3.0° and 4.2° S Latitude (Figure 1) in the Upper Pangani River Basin, northeastern Tanzania. The catchment has a total drainage area of about 3300 km^2. The Ruvu River catchment has a semi-arid climate, with an annual mean temperature of 23 °C and average annual precipitation of approximately 2000 mm along the slopes of Mt. Kilimanjaro to 500 mm in the lowlands (PBWO/IUCN, 2007a). Most of the precipitation occurs from March to May (*Masika* season) (Kiptala et al., 2013) and varies considerably among years.

Land use follows the escarpment with Afrotropical montane rain forest along the slope of Mt. Kilimanjaro forest reserve, and multi-strata agroforestry (with intercropped coffee and banana plantations as main crops, and livestock keeping including dairy cattle, goats and pigs) in the upper reaches (Mathew et al., 2016). The middle and lower reaches consist of savanna bushland, bare land, small and large scale irrigated agriculture (commonly grown crops include rice, maize, beans, sisal, sugarcane, vegetables, and fruits), herding, fishing and small industries (UNDP, 2014; Mathew et al., 2016). About 80% of the population is engaged in agriculture, and irrigation consumes most of the available water resources up to 64% of the total blue water (Kiptala et al., 2013).

Numerous temporary pools varying in size, morphometry and hydroperiod have existed in the lowland of the Ruvu River catchment. However, there are no exact records of the total number of pools in the catchment. Unfortunately, most of the pools have been converted to agricultural land, settlement and/or filled-up (e.g. for mosquito control) (Mwaijengo *personal communication with local people*).

The study area contains two categories of temporary pools, i.e., endorheic and river connected pools. Endorheic pools have an independent hydrology and are not physically connected to any other aquatic system. River connected pools periodically connect with the Ruvu river when the flooding occurs, often on a seasonal basis. All temporary pools (i.e., endorheic and river connected pools) start to fill up at the start of the rainy season (March) and dry up in the dry season (from June to February). However, the timing and duration of filling episodes vary substantially between years, depending on the rainfall pattern. Some pools can remain inundated through to May, however, small endorheic pools are short-lived and dry-up within four weeks. Later, at the peak of the rainy season (April), river connected pools connect with the Ruvu River (i.e., when the river floods the flanking plains). The connectivity can last for few days to about two weeks depending on rainfall intensity and pool distance to the river (i.e., pools closer to the river channel are likely to be more frequently connected to the river with a more frequent exchange of nutrients, organisms, and sediments with the river compared to more distant pools). Generally, flooding of the Ruvu River occurs once a year at the peak of the rainy season (April), except for dry years when rainfall is relatively low and subsequently the water level in the Ruvu River become extremely low. All pools are not subjected to any environmental or water management and occur on a mixture of agricultural and settlement land.

2.2. Study design

We studied a cluster of twelve temporary pools in the Ruvu River catchment (Fig.1). The selection of pools was done largely based on their accessibility. Pool locations were recorded using a handheld GPS (Garmin eTrex 10, ± 3 m point accuracy). The set of studied pools comprises a strong gradient in hydrological connectivity (HC), with river connected pools seasonally connect to the Ruvu river during the high base flow while endorheic pools lack such connection. Five of the twelve selected temporary pools were river connected pools. Some of these pools directly connect to the river through erosion channels. All selected pools were visited once during the peak of the wet season of April 2017 to measure the environmental variables and to sample the macroinvertebrate communities. During the survey, river connected pools were already connected to the flooding Ruvu River, except one pool (pool F3) which was not connected. We treated pool F3 not as an outlier because the same pool may be connected in some years and not in others; depending on rainfall intensity, distance to the river and location in the landscape, as also explained above. When they do not connect, typical temporary pond characteristics and taxa may become apparent. Concurrently, we measured water quality variables and sampled macroinvertebrate communities in different sites along the Ruvu River.

In this study, connectivity encompasses two aspects; the hydrological connectivity (HC) which denotes the distance from the pool to the river (only river-connected pools), and pool connectivity (PoolCon) which represents the shortest distance to the nearest pool (between all pool pairs, for both endorheic and river connected pools).

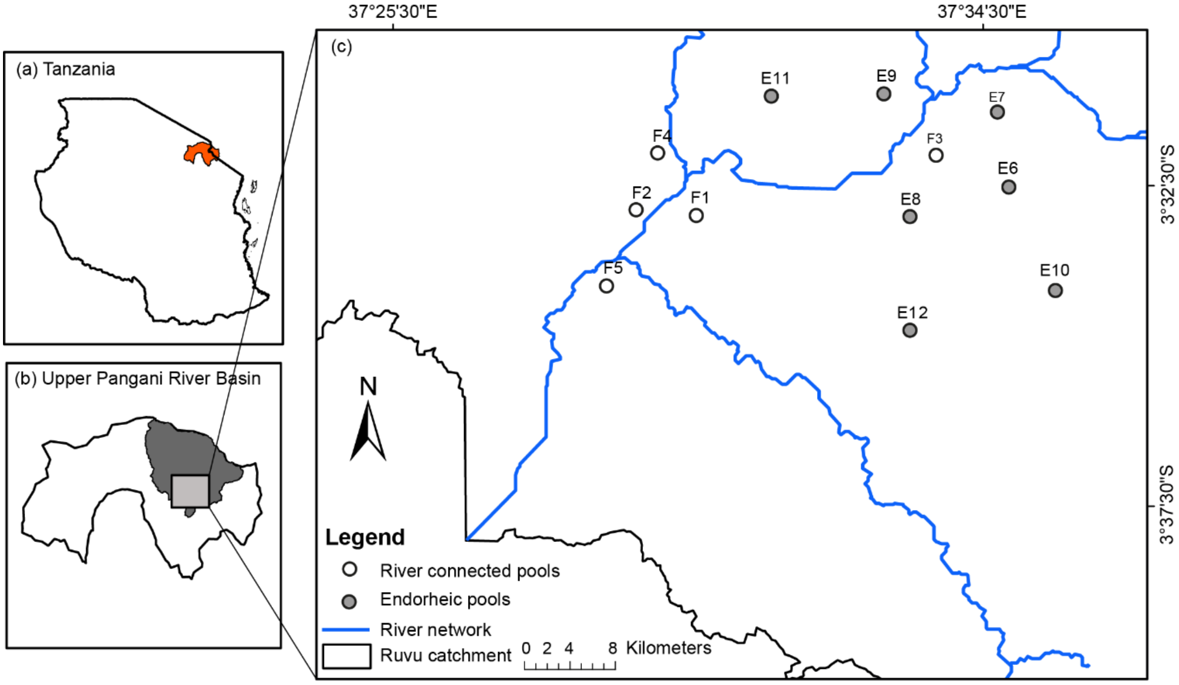

Fig.1 Map of the study area showing the location of temporary pools (endorheic pools = filled circles; river connected pools = unfilled circles) in the Ruvu River catchment, northeastern Tanzania. Insert: Map of East-Africa with the location of the Upper Pangani River Basin and the Ruvu River catchment.

2.3. Assessment of local habitat and environmental conditions

Daytime dissolved oxygen concentration (DO) and temperature (Temp) were measured *in situ* using a portable HANNA multi-parameter probe (Model-HI 9829). Conductivity (EC) and pH were measured using a portable HANNA multi-parameter probe (Model-HI 9829) in an integrated water sample of 10 liter (taken at five different locations in the pool). Turbidity (Turb) was measured using a portable turbidity meter (HANNA-Model-HI93703). *In vivo* concentrations of chlorophyll-a (Chl_a) were measured using an AquaFluor Handheld Fluorometer (Model-8000-010). An integrated water sample of 10 liters for water quality analyses was prepared by collecting water at five different locations in the pool using a 2-liter plastic beaker. Water samples were collected in 1-liter polyethylene plastic bottles and transported in an iced cooler box to the laboratory of the Department of Water Environmental Science and Engineering (WESE) at the Nelson Mandela African Institution of Science and Technology (NM-AIST), Arusha, Tanzania for analyses. The samples were stored at 4 °C until further analysis.

Chemical analysis of total nitrogen (TN), total phosphorus (TP), orthophosphate (PO_4^{-3}), nitrate (NO_3^--N), ammonium ($NH4^+$-N), and chemical oxygen demand (COD) were performed using a portable spectrophotometer (Model HACH-DR2800). Orthophosphate concentration was measured using an ascorbic acid (PhosVer 3) method (range: 0.02 to 2.50 mg/L PO_4^{3-}), nitrate concentration using a cadmium reduction method (range: 0.01 to 30.0 mg/L NO_3^--N), ammonium using a Nessler method (range: 0.02 to 2.50 mg/L ($NH4^+$-N), total phosphorus using PhosVer3 with acid persulfate digestion method (range: 0.06 to 3.50 mg/L PO_4^{3-}), total nitrogen using a persulfate digestion method (range: 0.1 to 25.0 mg/L N), and chemical oxygen demand by means of a reactor digestion method (range: 0.7 to 150.0 mg/L COD). Digestions were carried out using a COD reactor (HACH-DRB200). All chemical analyses followed the standard methods for the examination of water and wastewater by APHA (2012).

Depth of each pool was measured using a graduated measuring stick at three different locations in the pool basin to get an average depth (Avdep). Surface area was estimated with a GPS (Garmin eTrex 10) by walking the perimeter of the pool. For small pools, dimensions were measured with a tape meter. Pool connectivity (PoolCon) was determined as the shortest distance to the nearest pool (between all pool pairs) and hydrological connectivity (HC), for river connected pool, as the distance from the pool to the river based on geographic coordinates in ArcGIS 10.2.2 desktop GIS software (ESRI Company, Redlands, California, USA). The short HC indicates that a pool is closer to a river and thus will connect more easily (probably every season) and remain connected for a longer time. Total percentage macrophyte cover (i.e., emergent, submerged, and floating) was assessed by visual estimates on a scale 0-4: 0= <5%, 1= 5%–25%, 2=26%–50%, 3= 51%–75%, and 4=76%–100%, following (Waterkeyn et al., 2008). The visual estimate of macrophyte cover was carried out by one person throughout the sampling to minimize judgment biases.

2.4. Sampling and identification of macroinvertebrates

Macroinvertebrates were collected in a semi-quantitative way by sweeping a 500-µm D-frame net 15-20 times across different microhabitats in the pool (i.e., open water, submerged vegetation, floating vegetation, and emergent vegetation) relative to the structural heterogeneity and pool size. This standardized semi-quantitative method allowed direct comparisons across pools. All collected material was transferred to a labeled collecting jar and preserved using 70% ethanol. In the laboratory, all macroinvertebrates were sorted from detritus and preserved in 70% ethanol. Large branchiopods were identified to species level (expect *Branchipodopsis* sp. to genus level), while other macroinvertebrates were identified to genus level under a stereomicroscope (Olympus 12, Olympus Optical Co. Ltd., Tokyo, Japan) using various identification guides (Day et al., 1999; Day and De Moor, 2002; Day et al., 2002; De Moor et al., 2003; Stals and De Moor, 2007; De Moor et al., 2009). Functional feeding groups (FFG) were assigned to all identified macroinvertebrates based on feeding ecology, using various guides (Davies and Day, 1998; Merritt and Cummins, 1996; Hawking et al., 2006). The groups were collector-gatherer (CG), collector-filterer (CF), predator (PR) and scrapper (SC). The number of fishes caught in the macroinvertebrate net (500µm D-frame net) was used as an extra explanatory variable in the analyses.

River sampling was done using a 1mm-D frame net. The macroinvertebrates were sampled from the dominant habitat type at each site (i.e., the habitat that covers about 70% of the 50 m stretch making up the river section at the site). The stones (a collective term for bedrock, boulders and cobbles) and gravel/sand/mud (GSM) habitats were sampled for one minute. The kick-net was placed in the river in the opposite direction of current flow. Then the riverbed was agitated continuously using the sampler's feet for one minute to dislodge specimens, while continuously sweeping the net through the disturbed area to collect the macroinvertebrates. The vegetation habitat was sampled by pushing the net vigorously and repeatedly against and through the vegetation over an area of approximately two meters. Further processing of samples took place in the laboratory with taxa identifications to family level using various identification guides as indicated above. Although species level identification is desirable, several riverine studies have demonstrated that the use of family level classification for macroinvertebrates can produce meaningful information (Kaaya et al., 2015; Fugère et al., 2016; Dalu et al., 2017).

2.4. Data analyses

We first calculated general diversity indices (alpha-α, beta-β, and gamma-γ) on the macroinvertebrate abundance data. Taxon richness was used as a measure of diversity. Alpha (local) diversity was calculated as taxon richness per pool. Gamma (regional) diversity was measured as the total taxon richness of the entire set of sampled pools. Beta diversity (community differentiation between pools) was first calculated using the Baselga Jaccard (DJ) dissimilarity of species presence-absence (Baselga, 2010; Baselga and Orme, 2012) using the function *beta.multi* of the 'betapart' package in R (version 3.1.2, R Core Team 2014). In addition, we partitioned β-diversity into nestedness (Nes_{BJ}) and turnover (Rep_{BJ}) components following (Baselga and Orme, 2012; Legendre, 2014). *Nestedness* here denotes difference in taxon richness pattern between sites characterized by a pattern whereby the species at a poorer site (small number of species) are a strict subset of the species at a richer site. *Turnover* implies the spatial replacement of some species by others as a consequence of environmental or spatial sorting, regardless of possible differences in species richness between the pools (Baselga, 2010; Legendre, 2014). To test for homogeneity of multivariate dispersions between endorheic and river connected pools, we computed an additional measure of β-diversity as the average distance to the group centroids in multivariate space, using the function *betadisper* in R (version 3.1.2, R Core Team, 2014) from the 'vegan' package (Anderson, 2006 and Anderson et al., 2006). Multivariate dispersion is a powerful approach to determine the variability in species composition and can be considered as a broad β-diversity measure (Anderson et al., 2006; Jiang et al., 2016). To test for any significant differences in alpha diversity (taxon richness) and functional feeding group richness between river connected and endorheic pools, we computed a t-test at 95% confidence level.

To uncover whether there are consistent differences in environmental conditions between endorheic and river connected pools, we first computed a multivariate analysis of variance on environmental variables using the function *adonis* on a Euclidean distance matrix from the 'vegan' package in R (version 3.1.2, R Core Team, 2014). Second, we performed t-tests to test for any significant differences in environmental variables between pool types. Principal component analysis (PCA) was used to visualize the spatial variation in environmental variables and macroinvertebrate assemblages (Hellinger transformed abundance data) of endorheic versus river connected pools. Environmental variables: EC, DO, turbidity, pool surface area and nitrate were first log (x) transformed prior to analyses to improve the normality of the data.

We used redundancy analyses (RDA) to study the relationship between environmental factors and macroinvertebrate community structure. Abundance data were Hellinger transformed prior to the RDA analysis to improve the performance of ordination with community composition data containing many zeros (Legendre and Gallagher 2001; Zuur et al. 2007). Statistical significance was assessed using Monte Carlo permutation tests (nperm= 999). To determine the subset of environmental variables explaining most variation in community structure between pools, a forward selection procedure was performed. We a *priori* excluded from the analysis rare taxa that occurred in only one pool as their occurrence cannot be modeled. To correct for the differences in habitat type, we included pool type (endorheic or river connected) as a categorical predictor variable in the model. We used PCA ordination diagrams to visualize the relationship between macroinvertebrate community composition (using Hellinger transformed abundance data) and the most important environmental variables (variables with the highest explanatory power retained in the model by forward selection) plotted as supplementary variables. The analysis was first performed for the full data set containing both endorheic and river connected pools. To examine the importance of temporary connections (hydrological connection) with the river as a driver of community patterns the same analysis was performed on a reduced data set excluding the endorheic pools. The hydrological connectivity (i.e., the distance from the pool to the river) was included as an environmental predictor in the model. The actual hydrological connection during sampling was included as a binomial variable (i.e., 0 = not connected and 1 = connected) in the model.

We built a generalized linear model with Poisson error distribution to study the relationship between taxon richness (α-diversity) and environmental variables using the *glm* function of the vegan package in R (version 3.1.2, R Core Team, 2014). A backward selection followed by a forward selection was computed to eliminate the non-significant environmental variables from the model using the function *step* in the vegan package (Oksanen et al., 2016). The Akaike information criterion (AIC) and Mc Fadden's pseudo R^2 coefficient (R^2_{pseudo}) were used to determine the model with the best subset of predictor environmental variables.

Finally, we applied the indicator species method (i.e., IndVal) to determine indicator taxa linked to the two different pool (habitat) types (Dufrêne and Legendre 1997; De Cáceres et al. 2010). The studied pools were grouped *a priori* into river connected pools and endorheic pools. A good indicator taxon is expected to occur in most pools from a specific type (river connected versus endorheic). The indicator species method calculates an (IndVal) index of association between the species and each habitat type and identifies the highest association value (Dufrene and Legendre 1997). The indicator value of a taxon varies between 0 and 1, attaining its maximum value when all individuals of one taxon occur in all sites of a particular habitat type (Dufrêne and Legendre 1997; Heino et al. 2005; Lumbreras et al. 2016). The indicator value comprises two components; (i) a specificity/predictive value (component A) and (ii) a sensitivity/fidelity (component B). Specificity (A) is the probability that the surveyed site belongs to the target habitat type given the fact that the taxon has been found, while sensitivity (B) is the probability of finding the taxon in sites belonging to a specific habitat type. This approach allows the comparison of indicator values between unrelated taxa because values are calculated independent from other species present in the assemblage (Dufrene and Legendre 1997). The significance of the taxon-specific indicator values was tested via Monte-Carlo permutations (nperm=999).

Prior to these analyses, correlations between environmental variables were tested using the Spearman correlation to prevent multicollinearity in the models. If variables were significantly correlated, only the most relevant environmental variable was retained. All analyses were performed in R (version 3.1.2, R Core Team, 2014) using the package vegan, betapart, abind, vcd, permute, indicspecies and packfor.

3. Results

A total of 2293 macroinvertebrates corresponding to 31 taxa were recorded over all twelve temporary pools (regional or gamma diversity) in the Ruvu River catchment (Table 1): 13 hemipterans, 4 anisopterans, 2 zygopterans, 5 coleopterans, 2 decapod, 2 ephemeropterans, and 3 anostracans. Typical riverine macroinvertebrate taxa such as the hydrophilid beetles *Berosus sp*., atyid shrimps *Atyopsis* sp., and mayflies *Baetis* sp. were found only in floodplain pools. Regarding the large branchiopod anostracans, we only found species of the genera *Streptocephalus* and *Branchipodopsis*. *Notonecta* and *Anisops* species were the most abundant taxa occurring in all surveyed pools with especially a dominant representation in endorheic pools. Eight pools (67 %), contained at least one species of *Streptocephalus*. In general, anostracan species were not collected from river connected pools, except for river connected pool F3 (which was not connected to the river during the survey) housing two *Streptocephalus* species. The overall average alpha richness per pool was 9 (SD ±3.4). The list of macroinvertebrate taxa found in the Ruvu River is provided in the supplementary information (Table S1).

Minimum, maximum, mean and standard deviation values for macroinvertebrate taxon richness (alpha diversity) for all sampled pools are presented in Table 2. Alpha diversity was significantly higher in the endorheic than in the river connected pools ($t = -2.31$, $p = 0.02$), while beta diversity was higher in the river connected ($D_J = 0.73$) compared to endorheic pools ($D_J = 0.39$), (heterogenous of multivariate dispersions; F= 8.86, *p* = 0.03) (Fig. 2b). Overall, beta diversity (over all pools) was high ($D_J = 0.87$) and was largely explained by spatial taxon turnover ($Rep_{BJ} = 0.80$), rather than by nestedness ($Nes_{BJ} = 0.07$). Functional taxon richness based on feeding ecology was comparable between habitats. Predators dominated functional richness in both habitats, but their representation was relatively lower in the river connected pools. Collector-filterers and collector-gatherers were on average the second most important feeding groups in both habitats. Collector-gatherers and scrappers taxon richness were significantly different between pool types (t = 3.67, *p* = 0.003; t = 4.05, *p* = 0.001, respectively).

Table 1 Presence-absence of macroinvertebrates in temporary pools (endorheic and river connected pools) of the Ruvu River catchment. Functional feeding group (FFG) classification: collector-gatherer (CG), collector-filterer (CF), predator (PR) and scrapper (SC).

		Temporary Pools												**FFG**
		Floodplain pools					**Endorheic pools**							
Macroinvertebrates		1	2	3	4	5	6	7	8	9	10	11	12	
Anisoptera	*Trithemis* sp.	+					+			+			+	PR
	Anax imperator		+											PR
	Crenigomphus sp.							+		+	+			PR
	Notogomphus sp.			+				+	+	+	+	+	+	PR
Zygoptera	*Lestes* sp.			+			+	+	+	+	+	+	+	PR
	Pseudagrion spp.					+		+	+	+	+	+	+	PR
Hemiptera	*Limnogeton* sp.	+												PR
	Agraptocorixa sp.	+												CF, PR
	Appasus spp.				+					+			+	PR
	Neomacrocoris sp.			+	+		+		+		+		+	PR
	Notonecta sp.	+	+	+	+	+	+	+	+	+	+	+	+	PR
	Macrocoris sp.	+			+									PR
	Enithares sp.		+		+					+	+		+	PR
	Anisops sp.	+	+	+	+	+	+	+	+	+	+	+	+	PR
	Micronecta sp.			+		+			+		+			CG
	Lethocerus sp.	+												PR
	Borborophilus sp.			+					+	+	+	+	+	PR
	Ranatra sp.			+			+							PR
	Laccotrephes sp.									+	+		+	PR
Coleoptera	*Spercheus* sp.			+			+							CF, PR
	Dineurus sp.			+	+				+	+	+			PR,
	Berosus sp.	+												CG, PR
	Dytiscus sp.			+			+				+			PR
	Hydrophilus sp.				+				+					CG, PR
Decapoda	*Atyopsis* sp.		+											CF, SC
	Caridina nilotica	+				+								CF, CG
Ephemeroptera	*Baetis* sp.	+	+		+									CG, SC
	Manohyphella sp.	+												CG, SC
Anostraca	*S. bourquinii*			+			+	+	+	+	+	+	+	CF
	S. wirminghausi			+			+	+	+	+	+	+	+	CF
	Branchipodopsis sp.							+	+		+	+		CF
Taxon richness		11	6	13	8	5	10	9	13	14	16	8	13	

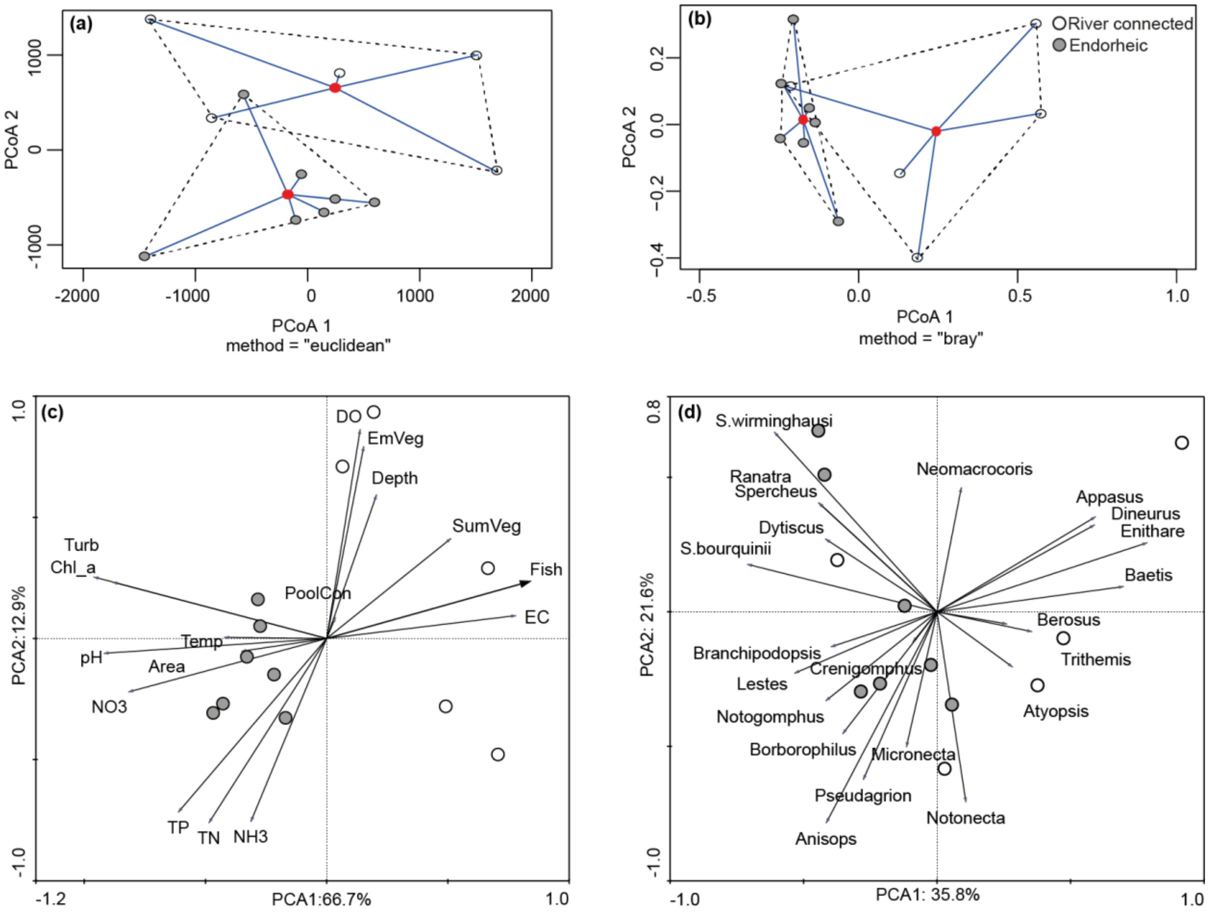

Fig. 2 Plots of multivariate homogeneity of group dispersion (betadisper at $p \leq 0.05$) on (a) Euclidean and (b) Bray–Curtis distances of environmental variables and macroinvertebrate abundance, respectively, and ordination biplots of principal component analysis illustrating the variation in (c) environmental variables and (d) macroinvertebrate abundance (Hellinger transformed abundance data) of temporary pools in the Ruvu River catchment. The first two principal component axes (PCA1 and PCA2) explained 79.6% and 57.4% of total variation in environmental variables and macroinvertebrate abundance, respectively. Presence of fish was plotted as supplementary variable not to influence the ordination (on environmental variables PCA). The blue line (on betadisper plots) denotes pool dispersion from the centroid. Filled circles represent endorheic pools and non-filled circle river connected pools. Depth = Average pool depth, Area= pool surface area, DO=Dissolved oxygen, SubVeg = Submerged macrophytes, EmVeg = Emergent macrophytes, NO3 = Nitrate, Temp= Temperature, Turb=Turbidity, Chl-a= Chlorophyll-a, TN= Total nitrogen, PoolCon = Pool connectivity, NH4 = Ammonium, TP= Total phosphorus.

Minimum, maximum, mean and standard deviation values of the measured environmental variables are presented in Table 2. Nutrients (i.e., ammonium, nitrate, total nitrogen, orthophosphate and total phosphorus) varied significantly (t-test, $p < 0.05$) between river connected and endorheic pools, with endorheic pools having higher nutrient concentrations (Table 2, Fig. 3). Significant differences (t-test, p

< 0.05) were also observed for turbidity, chlorophyll a, pH and electric conductivity, with high mean ion concentrations (i.e., EC) in the river connected pools, while high turbidity, pH and chlorophyll a concentration in endorheic pools (Table 2, and Fig. 3). River connected pools were relatively deeper (mean depth = 57.12cm ± 13.99 SE) compared to endorheic ones (mean depth = 39.52cm ± 4.54 SE). Endorheic pools were generally larger (mean log (Area m^2) = 3.51± 0.03 SE) compared to river connected ones (mean log (Area m^2) = 3.35±0.10 SE). A multivariate analysis of variance on environmental variables also revealed significant differences between river connected and endorheic pools (heterogenous of multivariate dispersions; $R^2 = 0.12$, F= 1.35, $p = 0.028$). Environmental characteristics showed higher dispersion (variance) in river connected pools than in the endorheic pools (Fig. 2a). The summary statistics of the measured physico-chemical water quality variables along the Ruvu River are presented in Table S2 (Supplementary Information).

Table 2 Descriptive statistics and t-test results (indicating differences between floodplain and endorheic pools) for environmental variables and taxon richness in temporary pools of the Ruvu River catchment. Significant differences ($p < 0.05$) are highlighted in bold. ***= $p < 0.001$, ** = $p < 0.01$, and * = $p < 0.05$. Min=Minimum, Max=Maximum, SD = Standard deviation, t = t-statistics, p = p-values, EC=electric conductivity, Area = Pool surface area , Depth = Average pool depth , DO=Dissolved oxygen, SubVeg = Submerged macrophytes, EmVeg = Emergent macrophytes, Temp= Temperature, Turb=Turbidity, PO_4^{3-} = Orthophosphate, NO_3^- = Nitrate, Chl-a= Chlorophyll-a, $NH4^+$ = Ammonium, TN= Total nitrogen, PoolCon = Pool connectivity, and TP= Total phosphorus.

	River Connected Pools				**Endorheic Pools**				**t-test**	
Variables	Min	Max	Mean	SD	Min	Max	Mean	SD	t	*p*
Log (Area) (m^2)	3.09	3.59	3.35	0.23	3.41	3.67	3.51	0.08	-1.63	0.13
Depth (cm)	21.7	91.1	57.16	31.28	27.9	59.2	39.52	12.03	1.38	0.19
Temp(°C)	24.5	26.23	25.43	0.63	24.2	28.5	26.51	1.59	-1.41	0.18
pH	7.92	9.12	8.25	0.50	8.74	9.96	9.30	0.43	**-3.9**	**0.003****
Log (EC) (µS/cm)	2.99	3.49	3.21	0.18	2.84	3.33	3.0	0.15	**2.37**	**0.038***
Log (DO) (mg/L)	0.50	0.80	0.66	0.13	0.50	0.61	0.57	0.05	1.87	0.09
Log (Turb) (ftu)	1.30	3.09	2.02	0.74	2.50	3.04	2.88	0.18	**-2.97**	**0.01***
Chl-a (µg/L)	119.6	366.6	193.2	107.38	243.5	402.5	332.0	51.51	**-3.01**	**0.01***
EmVeg (% cover)	0.00	0.68	0.40	0.28	0.00	0.31	0.16	0.13	1.93	0.08
SubVeg (% cover)	0.00	0.56	0.31	0.24	0.00	0.45	0.13	0.16	1.56	0.15
Log (NO_3^-) (mg/L)	0.28	0.97	0.50	0.27	0.97	1.36	1.10	0.14	**-4.97**	**< 0.001*****
$NH4^+$(mg/L)	2.25	4.22	3.01	0.75	4.27	2.05	11.13	6.57	**-2.71**	**0.02***
PO_4^{3-}(mg/L)	0.72	5.66	3.5	2.06	8.64	20.53	12.6	3.90	**-4.71**	**< 0.001*****
TN (mg/L)	3.10	7.10	4.92	1.45	5.60	15.20	10.74	3.09	**-3.88**	**0.003****
TP (mg/L)	1.10	4.93	2.89	1.61	9.60	14.6	12.34	1.87	**-9.10**	**< 0.001*****
PoolCon (m)	1.31	2.15	1.79	0.34	1.01	3.69	2.09	1.08	-0.58	0.57
Taxon richness	5.00	13.00	8.60	3.44	9.00	16.0	11.86	2.43	**-2.31**	**0.02***

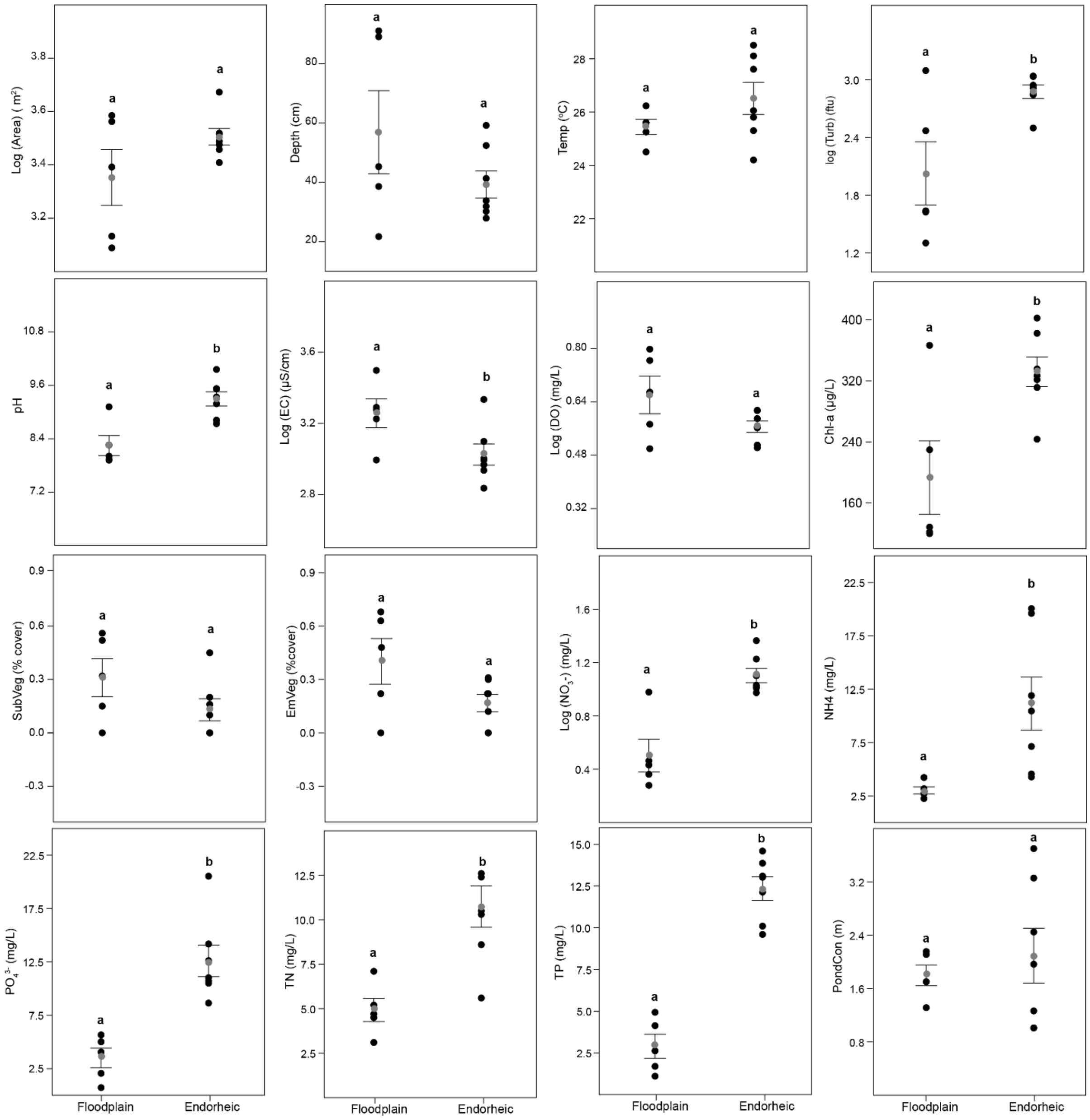

Fig. 3. Graphs of the variation in environmental variables between endorheic and floodplain pools in the Ruvu River catchment. **aa** indicates no-significant difference, **ab** indicates significant difference (based on t-test at $p \leq 0.05$), black circles represent real datapoints, gray circles mean values, and error bars represent standard errors of the mean. Abbreviations: EC=electric conductivity, Chl-a=chlorophyll-a, Turb=turbidity, Temp= temperature, DO = dissolved oxygen, PO_4^{3-}= orthophosphate, NO_3^{-} N=nitrate, $NH4^{+}$-N=ammonia, TP=total phosphorus, TN=total nitrogen, Depth= average depth of the pool, Area= surface area of the pool, SubVeg= Submerged macrophytes, EmVeg= Emergent macrophytes, and PoolCon=pool connectivity.

Principal component analysis (PCA) illustrated spatial variation in environmental variables and macroinvertebrate assemblages among pools. PCA axes 1 and 2 together explained 79.6% and 57.4% of total variation in the environmental characteristics and macroinvertebrates, respectively (Fig. 2 c, d). For environmental variables, PC1 captured most variation in nutrient concentrations, pH and chlorophyll-a, whereas PC2 represented variation in dissolved oxygen, emergent vegetation, turbidity, and depth (Fig. 2c and Table S2). River connected pools were highly associated with presence of fish, higher dissolved oxygen, higher electric conductivity and vegetation cover, and were relatively deeper compared to endorheic pools. In contrast, endorheic pools were associated with higher nutrient concentrations, higher turbidity and higher chlorophyll-a concentration. For macroinvertebrates, PC1 captured most of the variation in macroinvertebrate assemblages (35.8%) (Fig. 2d). Macroinvertebrate taxa that were positively associated with river connected pools included mayflies *Baetis* sp., hydrophilid beetles *Berosus* sp., libellulid dragonflies *Trithemis* sp., belostomatin water bugs *Appasus* sp. and atyid shrimps *Atyopsis* sp. Endorheic pools were positively associated with fish predation sensitive taxa such as *S. bourquinii, S. wirminghausi*, *Branchipodopsis* sp. (anostracans), damselflies *Lestes* sp., *Pseudagrion* sp., dragonflies *Crenigomphus* sp., *Notogomphus* sp., nepid water scorpions *Borborophilus* sp., *Ranatra* sp., and water scavenger beetles *Spercheus* sp.

RDA analysis revealed a significant association of environmental variables with macroinvertebrate assemblages in the studied temporary pools (F= 2.61, p = 0.003) (Table 3). Average depth of the pools and presence of fish emerged as the most important environmental variables determining macroinvertebrate assemblages. The RDA model explained 23% of the total variation in the composition of macroinvertebrates. Exclusion of endorheic pools from our analysis resulted in a model in which emergent macrophyte cover and fish explained a significant proportion of the composition of macroinvertebrate assemblages (21%) of the river connected pools (Table 3). The water boatmen *Micronecta* sp., backswimmers *Notonecta* sp., *Anisops* sp., nepid water scorpions *Borborophilus* sp., and damselflies *Pseudagrion* sp., were more likely to be found in deep pools and pools that contain more macrophytes. The anostracans *S. bourquinii,* and *S. wirminghaus*, nepid water scorpions *Ranatra* sp., and water scavenger beetles *Spercheus* sp. were positively associated with pools without fish. The PCA ordination bi-plot visualizing the relationship between macroinvertebrate community composition (Hellinger-transformed macroinvertebrates abundance data) and the most important environmental variables (retained in the forward selection plotted as supplementary variables) for all pools and river connected pools is presented in Fig. 3.

Table 3 Results of the RDA analyses showing the global F, p-value and coefficients of determination ($R^2_{Adjusted}$) of the full models, and F-statistic and p-value of the selected important environmental variables explaining macroinvertebrate assemblages in the temporary pools in the Ruvu River catchment. The models are based on a forward selection procedure aimed to maximize the potential variation in macroinvertebrate assemblages that can be explained by environmental variables. Significance levels are indicated using *** = p < 0.001, ** = p < 0.01, and * = p < 0.05.

Pools	**Environmental Variables**	**F**	**p value**	**Global F**	**p value (global F)**	**$R^2_{Adjusted}$**
All pools	Depth	2.13	0.033*	2.61	0.003**	0.23
	Fish	3.10	0.002**			
River connected pools	Emergent macrophytes	2.34	0.036*	2.07	0.02*	0.21
	Fish	1.94	0.041*			

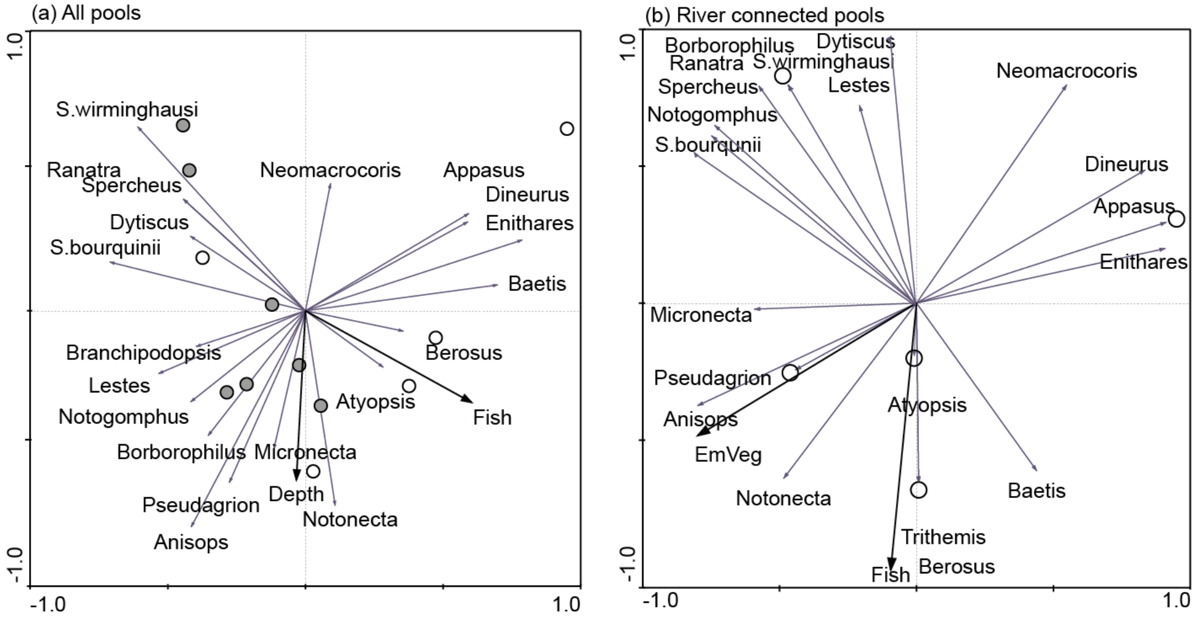

Fig.3. Ordination bi-plot of principal component analysis (PCA) with (a) all pools and (b) river connected pools, illustrating the relationship between the most important explanatory (environmental) variables (retained after forward selection in the RDA models) and macroinvertebrate community composition (Hellinger transformed macroinvertebrate abundance). Important environmental variables were plotted as a supplementary variable to not influence the ordination. Black arrows represent significant environmental variables. Filled circles represent endorheic pools and non-filled circles represents river connected pools.

The most important environmental variables retained by generalized linear models explaining the variation in taxon richness among pools are presented in Table 4. The model explained 21% of the variation in taxon richness. Macroinvertebrate taxon richness was positively affected by chlorophyll-a, submerged macrophytes and dissolved oxygen, and negatively affected by nutrients (nitrate) and electric conductivity.

Table 4 Results of the generalized linear models with AIC and coefficients of determination R^2_{Pseudo} (of the selected model), z-statistic and p-value of the most important environmental variables of the selected model for macroinvertebrate taxon richness in the temporary pools of the Ruvu River catchment. The model is based on backward followed by forward selection procedure aimed to maximize the potential variation in taxon richness that can be explained by environmental variables. Significance levels are indicated using ***= p < 0.001, ** = p < 0.01, and * = p < 0.05. A (+) sign refers to a positive association, (-) sign refers to a negative association.

Explaining variables	Coefficients	z-value	*p*-value	AIC (Full model)	R^2_{Pseudo}
Electric conductivity	-1.273	-2.476	0.013*	63.17	0.21
Dissolved oxygen	-0.034	-2.196	0.028*		
Chlorophyll-a	1.517	3.161	0.001**		
Submerged macrophyte	1.298	2.752	0.011*		
Nitrate	-0.081	-2.263	0.023*		

Indicator taxa analysis revealed *Baetis* spp. as an indicator taxon for floodplain pools (Table 4); it occurred only in floodplain pools (A = 1.0), but not in all of them (B = 0.614). In contrast, *Lestes* sp., *S.wirminghausi* and *Pseudagrion* sp. stood out as indicator taxa for endorheic pools (Table 4). *Lestes* sp. occurred in all endorheic pools (B = 1.0) and was largely restricted to it (A = 0.975). *S.wirminghausi* occurred in most of the endorheic pools (B = 0.856) to which it was largely (but not completely) restricted (A=0.967). Similarly, *Pseudagrion* sp. occurred in most of the endorheic pools (B = 0.857) to which it was not completely restricted (A= 0.887).

Table 5 Results of the macroinvertebrate indicator taxon analysis listing indicator taxa for each temporary pool habitat type (i.e., river connected and endorheic pools). Indicator values and associated *p* values are provided as well as the specificity (A) and sensitivity (B) scores. Significance levels are indicated as follows: ** = p < 0.01, and * = p < 0.05.

Temporary Pools	**Indicator taxa**	**Indicator Value**	**p value**	**A**	**B**
River connected	*Baetis* sp.	0.775	0.04*	1.0	0.614
Endorheic	*Lestes* sp.	0.988	0.004 **	0.975	1
	S. wirminghausi	0.911	0.01 **	0.967	0.856
	Pseudagrion sp.	0.872	0.02 *	0.887	0.857

4. Discussion

Here, we assessed the role of seasonal river connections in modulating macroinvertebrate community structure by comparing river connected with endorheic temporary pools in the Ruvu River Catchment, northeastern Tanzania. As we initially predicted in our hypotheses, there was a clear difference in macroinvertebrate communities between endorheic and river connected pools, with different sets of indicator taxa emerging for the two temporary pool types. Seasonal river connections affected environmental conditions in the river connected pools with especially higher electric conductivity and lower nutrient concentrations. In addition, the river facilitated the dispersal of fish which excluded predation sensitive taxa such as fairy shrimps.

Typical riverine macroinvertebrate taxa such as the mayflies *B. harrisoni*, hydrophilid beetles *Berosus* sp., and atyid shrimps *Atyopsis* sp. only occurred in river connected pools. This is in line with the FPC which indicates that lateral hydrological connectivity facilitates dispersal and exchange of organisms between the river channel and the connected floodplain water bodies (Junk et al., 1989). Several studies on river-floodplain ecosystems confirmed the transport of riverine species to the floodplain wetlands by seasonal river connections (Bornette et al., 1998; Tockner et al., 1999a; Amoros and Bornette, 2002; Gallardo et al., 2014). Dube et al. (2019), for example, reported a higher number of riverine macroinvertebrates in highly connected temporary floodplain wetlands than in poorly connected ones in the Phongolo floodplain in South Africa. Similarly, river overflows have been reported to disperse plant propagules in floodplain wetlands (Bornette et al., 1998; Rooney et al., 2013). Endorheic pools in our study, in contrast, supported fish predation sensitive taxa such as the fairy shrimps *Streptocephalus bourquinii*, *Streptocephalus wirminghausi* and *Branchipodopsis sp.*, and a higher proportion of macroinvertebrate predator taxa. These findings are similar to Nhiwatiwa et al. (2017) who recorded a higher abundance of predators such as Corixidae, Notonectidae, and Dytiscidae in endorheic pans compared to floodplain pans in the south-eastern Lowveld of Zimbabwe. The prevalence of actively migrating predator taxa in endorheic pools illustrates the relative importance of dispersal in determining community composition in freshwater habitats. The high abundance of predatory macroinvertebrates even in small endorheic pools, however, contradicts the idea that pools with short hydroperiods exclude predators while longer hydroperiods provide more opportunities for predators to colonize (Spencer, 1999; O'Neill and Thorp, 2014).

Interestingly, while earlier studies demonstrated an increase in nutrient and turbidity levels in the floodplain wetlands after connection with the river (Junk et al.,1989; Tockner et al., 1999a; Thomaz et al., 2007; Weilhoefer and Pan, 2008), our results did not conform to this expectation. Rather, we found lower nutrient concentrations in river connected pools compared to the endorheic ones. The low nutrient concentrations in river connected pools may be a result of in one hand receding flood waters which channel back nutrients and organic matter from the floodplain into the main river channel (Junk et al., 1989) and on the other hand high hydrological connectivity between river and floodplain habitats which leads to dilution of floodplain conditions including nutrient concentrations (Tockner et al., 1999a; Dube et al., 2019). This is because the effect of the incoming river water in floodplain habitats is to a large extent dependent on the timing, duration and magnitude of flooding (Amoros and Bornette, 2002; Weilhoefer et al., 2008; Agostinho et al., 2009). The elevated electrical conductivity in the river connected compared to endorheic pools in our study could be attributed to the higher electric conductivity from the flooding water. The average electrical conductivity was 1478 μS/cm and 1594 μS/cm in the Ruvu River and river connected pools respectively compared to 1012.5 μS/cm in the endorheic pools. A previous study in the Ruvu River catchment also detected higher levels of electric conductivity in the Ruvu River compared to other rivers in the catchment (Mwaijengo et al., 2020).

Overall, macroinvertebrate alpha diversity in endorheic pools (mean richness=11.86) was higher compared to river connected pools (mean richness=8.60). The absence of large branchiopods in river connected pools was probably due to fish predation, as the hydrological connection with the river channel facilitated fish dispersal. A strong negative impact of fish predation on large branchiopods in occasionally river connected pools is also supported by earlier studies (Waterkeyn et al., 2008; Nhiwatiwa et al., 2009, 2011; Dube et al., 2019). The large body size and active behavior of large branchiopods make them highly vulnerable to visual predators (Nhiwatiwa et al., 2011; Dube et al., 2019). The absence of fish in the isolated endorheic pools, not only resulted from spatial isolation but also from the more temporary nature of the aquatic phase eliminating fish without drought resistant life stages (Williams, 2006; Pinceel et al., 2015).

While endorheic pools supported higher alpha diversity, beta diversity (community dissimilarity between pools) was higher in river connected ($D_J = 0.73$) compared to endorheic pools ($D_J = 0.39$). A gradient in hydrological connectivity of river connected pools results in variation in environmental conditions and differences in locally sorted macroinvertebrate communities (Paillex., 2007; Gallardo et al., 2014; Dube et al., 2019; Larsen et al., 2019). This is in accordance with Amoros and Bornette (2002) who described that differences in the nature and intensity of hydrological connectivity contribute to the spatial heterogeneity of floodplain habitats, which results in high beta diversity. Castella et al. (1991) and Dube et al. (2019) also observed high beta diversity in floodplain wetlands of the Rhŏne River (France) and Phongolo River (South Africa), respectively. In addition, differences in environmental conditions driven by a gradient in lateral hydrological connectivity, provide complementary habitats required to complete life-cycles of different invertebrate species (Amoros and Bornette, 2002), resulting in species turnover in these systems. Functional feeding groups were comparable between endorheic and river connected pools, except scrapers and collector-gatherers that were more diverse in the river connected pools. The proportion of predatory taxa was higher in the endorheic pools than in the river connected pools. A similar significant increase in macroinvertebrate predators in endorheic pools was also found in a study that compared endorheic and floodplain pans in the south-eastern Lowveld of Zimbabwe (Nhiwatiwa et al., 2017).

Indicator species analysis showed substantial variation in indicator taxa between temporary pool types. This is consistent with our third hypothesis and indicates that different selection pressures limit the occurrences and resulting diversity of macroinvertebrates in both habitat types. *Baetis* sp. appeared as the only indicator taxon for the floodplain pools. The floodplain pools that were connected to the river did not contain any indicator taxon unique to temporary pool habitats. However, this does not mean that they are negligible from a conservation perspective. The same pools may be connected in some years and not in others. When they do not connect, fish may not colonize and possibly typical temporary pond taxa such as large branchiopods may still hatch from a dormant egg bank (Dube, 2017). In addition, the different pond types likely provide feeding grounds for different wetland birds that rely on different prey. For instance, piscivorous birds will benefit from fish that are trapped in a drying floodplain pond filled by the river. On the other hand, invertebrate feeding birds such as spoonbills and small waders will benefit from the large branchiopods that thrive in ponds that do not connect to the river. In endorheic pools, indicator species analysis revealed *Lestes* sp., *S. wirminghausi* and *Pseudagrion* sp. as indicator taxa. The finding of large branchiopods (i.e., *S. wirminghausi*) as indicators of endorheic pools also supports their flagship status for temporary pool habitats as also concluded by others (Brendonck et al., 2008; Van den Broeck, 2016). The studies of Lumbreras et al. (2016) and Dube et al. (2020) have also shown that large branchiopods could serve as indicators of good conservation status of temporary pools. These results underline the conservation value of endorheic pools for the region.

Other than habitat type, which had a dominant impact on the community structure of macroinvertebrates in (both endorheic and river connected) temporary pools in the floodplain of the Ruvu River catchment, variation in macroinvertebrate taxon richness and community structure were best explained by average pool depth, presence of fish, electric conductivity, chlorophyll-a, and submerged macrophyte. Pool depth is an ecologically important variable for macroinvertebrate communities, and often a proxy for the hydrological stability of the habitat (Brooks and Hayashi, 2002; Vanschoenwinkel et al., 2009;

Nhiwatiwa et al., 2011). This highlights the importance of the duration of the aquatic phase (hydroperiod) as a determinant of macroinvertebrate community processes in temporary pools, as also demonstrated in other studies (Brooks, 2000; Waterkeyn et al., 2008; Boven and Brendonck, 2009; Vanschoenwinkel et al., 2009; Bagella et al., 2010). In pools with on average a longer aquatic phase, more time is available for community development, completing life-cycles and successful colonization (Brooks, 2000; Waterkeyn et al., 2008; Boven and Brendonck, 2009). In addition, our finding on the importance of fish in explaining variation in macroinvertebrate assemblages in temporary pools also concurs with other studies (Waterkeyn et al., 2008; Wasserman et al., 2016; Nhiwatiwa et al., 2017; Dube et al., 2019). Macrophyte cover commonly has a positive effect on aquatic macroinvertebrates by enhancing the physical habitat structure, which improves food availability and provides shelter against predators (Nicolet et al., 2004; Nhiwatiwa et al., 2017). We found a negative relationship between electric conductivity and macroinvertebrate taxon richness. In similar studies where a strong gradient in conductivity was established, it also significantly affected macroinvertebrate diversity and community structure in temporary wetlands (Piscart et al., 2005; Boix et al., 2008; Waterkeyn et al., 2008, 2009). Chlorophyll-a concentrations (a proxy for phytoplankton biomass) also played a role in determining taxon richness, presumably because it reflects the availability of food resources for macroinvertebrates.

The high spatial variation (β-diversity) in macroinvertebrate communities in the temporary pools of the Ruvu River catchment was mainly the result of replacement (spatial turnover) rather than by nestedness (loss/gain). This result has an important management implication for the conservation of temporary pools in the region. In order to support higher regional biodiversity, we therefore recommend that conservation measures should focus on maintaining both endorheic and river connected temporary pool types. A similar approach was proposed based on other studies in different regions (e.g., Williams et al., 2003; Leibold et al., 2016; Dube et al., 2019). The findings of this study further confirm the notion that temporary pools and other small water bodies can contribute significantly to regional biodiversity. For example, some of the taxa recorded (e.g., *Streptocephalus* spp. and *Branchipodopsis* sp.) were typical of temporary waters and were not recorded before in permanent water bodies in the catchment (e.g., PBWO/IUCN, 2007; Mwaijengo et al., 2020). As such conservation measures should not only focus on large water bodies and ignore the small ones, which is a common practice in the study region.

Mosquitoes (*Anopheles, Culex, Aedes*), which are considered ecosystem disservices because they act as vectors for diseases such as Malaria and Dengue, were not captured/recorded in this study. There are two possible explanations for these observations. First, mosquitoes are known to avoid habitats containing predators (Blaustein et al., 2005; Vonesh and Blaustein, 2010), and likely avoid competition with other taxa by colonizing small, short hydroperiod ponds, or ponds in the early phases of inundation (Murrell and Juliano, 2013; Van den Broeck, 2016). This was partly confirmed in our study since predatory macroinvertebrates were more abundant even in small pools. This suggests that pools with relatively high biodiversity may reduce mosquito densities, due to competition and predation (Van den

Broeck, 2016). The absence of mosquitoes in the macroinvertebrate samples suggests that temporary floodplain pools may not be a desirable habitat for these taxa, as always deemed my local communities. Instead, highly ephemeral aquatic habitats, such as used tires, buckets, plastic bags, may therefore be a more suitable habitat for these taxa (Kling et al., 2007; Roiz et al., 2015; Hertz et al., 2016). Another possible explanation may be that the macroinvertebrate net mesh size 500-µm was too big to catch mosquito larvae. Therefore, we recommend future studies to use a macroinvertebrate net of mesh size 250-µm in order to capture more small invertebrate larvae.

It is also important to recognize that the current study has intrinsic limitations. First, our study is based on a single sampling event and does not capture temporal variation in community composition, which is often linked to temporal variation in environmental conditions (Nhiwatiwa et al., 2011). Secondly, sampling of active communities may be incomplete as we may have missed some taxa. An assessment of 'hidden diversity' by hatching resting egg banks in the sediments under controlled environmental conditions (Brendonck and De Meester, 2003) may provide higher resolution of macroinvertebrate species diversity in the studied area. Lastly, despite the study covered a large percentage of temporary pools in the catchment, the limited number of pools of each category may have resulted in limited statistical power and the observed low macroinvertebrate taxon richness.

Overall, our results confirmed that seasonal river connections modulate macroinvertebrate community structure in temporary pools, with river connected pools having different communities compared to endorheic pools in the same floodplain system. Flooding resulted in higher electric conductivity and lower nutrient concentrations and facilitated the transport of fish which excluded predation sensitive taxa. The high degree of spatial turnover in our study implies that conservation measures that aim to preserve temporary pool biodiversity should strive to include both endorheic and river connected pools in order to support higher regional biodiversity, potentially with a priority for the more diverse endorheic systems. The increasing demand for agricultural land (PBWO/IUCN, 2007b; Mathew et al., 2016) is contributing significantly to the disappearance of floodplain temporary pools in the catchment. There is, therefore, an urgent need for appropriate management strategies, including controlled access to agricultural land in the floodplain, by local authorities (i.e., Pangani River Basin is responsible for managing the water resources in the region) in order to reduce the further transformation of these vital habitats and loss of biodiversity. More importantly, we recommend the recognition and inclusion of small waterbodies, such as the temporary floodplain pools, in the decision-making process for effective biodiversity conservation and sustainable management of water resources in the region.

References

Amoros, C., Bornette, G., 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshw. Biol. 47, 761–776.

Anderson, M.J., 2006. Distance-Based Tests for Homogeneity of Multivariate Dispersions. Biometrics 62, 245–253.

Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9, 683–693.

APHA, 2012. Stand Methods for Examination of Water and Waste water, 22nd ed. ed. American Public Health Association,American Water Works Association,Water Environmental Federation, Washington, DC.

Bagella, S., Gascon, S., Filigheddu, R., Cogoni, A., Boix, D., 2016. Mediterranean Temporary Ponds : new challenges from a neglected habitat. Hydrobiologia 782, 1–10.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143.

Baselga, A. s, Orme, D.L., 2012. betapart : an R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812.

Blaustein, L., Blaustein, J., Chase, J.M., 2005. Chemical detection of the predator Notonecta irrorata by ovipositing Culex mosquitoes. J. Vector Ecol. 30, 299–301.

Boix, D., Biggs, J., Cereghino, R., Hull, A.P., Kalettka, T., Oertli, B., 2012. Pond research and management in Europe : “Small is Beautiful”. Hydrobiologia 689, 1–9.

Boix, D., Gascon, S., Sala, J., Badosa, A., Brucet, S., Lopez-Flores, R., Martinoy, M., Gifre, J., Quintana, X.., 2008. Patterns of composition and species richness of crustaceans and aquatic insects along environmental gradients in Mediterranean water bodies. Hydrobiologia 597, 53–69.

Bornette, G., Amoros, C., Lamouroux, N., 1998. Aquatic plant diversity in riverine wetlands : the role of connectivity. Freshw. Biol. 39, 267–283.

Brendonck, L., De Meester, L., 2003. Egg banks in freshwater zooplankton : evolutionary and ecological. Hydrobiologia 491, 65–84.

Brendonck, L., Michels, E., De Meester, L., Riddoch, B., 2002. Temporary pools are not “enemy-free”.In: Maeda-Martinez, A.M., B.V. Timms, D.C. Rogers, F.A. Abreu-Grobois & G. Murugan (Eds), Studies on Large Branchiopod Biology 4. Hydrobiologia 486: 147-159.

Brendonck, L., Rogers, C.D., Olesen, J., Weeks, S., Hoeh, W.R., 2008. Global diversity of large branchiopods (Crustacea : Branchiopoda) in freshwater. Hydrobiologia 595, 167–176.

Brendonck, L., Williams, W.D., 2000. Biodiversity in wetlands of dry regions (drylands) In: Biodiversity in wetlands: assessment, function and conservation vol. 1. Gopal, B., W.J. Junk & J.A. Davis (Editors). Backhuys Publishers, Leiden, The Netherlands, pp. 181-194.

Brooks, R.T., Hayashi, M., 2002. Depth-Area-Volume and Hdroperiod Relationships of Ephemeral (Vernal) Forest Pools in Southern New England. Wetlands 22, 247–255.

Calhoun, A.J.K., Mushet, D.M., Bell, K.P., Boix, D., Fitzsimons, J.A., Isselin-nondedeu, F., 2017. Temporary wetlands : challenges and solutions to conserving a “ disappearing ” ecosystem. Biol. Conserv. 211.

Castella, E., Richardot-Coulet, M., Roux, C., Richoux, P., 1991. Aquatic macroinvertebrate assemblages of two contrasting floodplains: The Rhŏne and Ain rivers, France. Regul. riversResearch Manag. 6, 289–300.

Chase, J.M., Ryberg, W.A., 2004. Connectivity , scale-dependence , and the productivity – diversity relationship. Ecol. Lett. 7, 676–683.

Dalu, T., Wasserman, R.J., Tonkin, J.D., Alexander, M.E., Dalu, M.T.B., Motitsoe, S.N., Manungo, K.I., Bepe, O., Dube, T., 2017. Assessing drivers of benthic macroinvertebrate community structure in African highland streams : An exploration using multivariate analysis. Sci. Total Environ. 601-602, 1340–1348.

Davies, B., Day, J., 1998. Vanishing Waters. University of Cape Town Press, Cape Town, Republic of South Africa.

Day, J.A., De Moor, I.J., 2002. Guides to the freshwater invertebrates of southern Africa. Arachnida and Mollusca (Araneae, Water Mites and Mollusca). Report No. TT182/02: 1–141, Water Research Commission, South Africa.

Day, J.A., Harrison, A.D., De Moor, I.J., 2002. Guide to the Freshwater Invertebrates of Southern Africa. Insecta III: Diptera. Report No. TT201/02: 1–200, Water Research Commission, South Africa.

Day, J.A., Stewart, B.A., De Moor, I.J., Louw, A.E., 1999. Guides to the freshwater invertebrates of southern Africa. Crustacea I : Notostraca, Anostraca, Conchostraca and Cladocera. Report No. TT121/00: 1–123, Water Research Commission, South Africa.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684.

De Meester, L., Declerck, S., Robby, S., Louette, G., Van De Meutter, F., De Bie, T., Michels, E., Brendonck, L., 2005. Ponds and pools as model systems in conservation biology , ecology and evolutionary biology. Aquat. Conserv. Mar. Freshw. Ecosyetems 15, 715–725.

De Moor, I.J., Day, J.A., De Moor, F.C., 2009. Guide to the Freshwater Invertebrates of Southern Africa. Insecta I: Ephemeroptera, Odonata and Plecoptera. Report No. TT 207/03:1-288, Water Research Commission, South Africa.

De Moor, I.J., Day, J.A., De Moor, F.C., 2003. Guide to the Freshwater Invertebrates of Southern Africa. Insecta II: Hemiptera, Megaloptera, Neuroptera, Trichoptera and Lepidoptera. Report No. TT214/03: 1–209, Water Research Commission, South Africa.

Dube, T., 2017. The Impact of Hydro-ecological variation on Aquatic Invertebrate Communities of South African Savanna Pans : Towards sustainable management of threatened ecosystems in the Ndumo . KU Leuven, Belgium.

Dube, T., de Necker, L., Wepener, V., Smit, N.J., Pinceel, T., Mwaijengo, G.N., Brendonck, L., 2020. A comparison of aquatic macroinvertebrate and large branchiopod community composition between temporary pans of a conservation area and surrounding communal area in South Africa. African Zool. 55, 1–11.

Dube, T., Pinceel, T., Necker, L. De, Wepener, V., Lemmens, P., Brendonck, L., 2019. Lateral hydrological connectivity differentially affects the community characteristics of multiple groups of aquatic invertebrates in tropical wetland pans in South Africa. Freshw. Biol. 1–15.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Fugère, V., Kasangaki, A., Chapman, L.J., 2016. Land use changes in an afrotropical biodiversity hotspot affect stream alpha and beta diversity. Ecosphere 7, 1–18.

Gallardo, B., National, S., Paillex, A., 2014. Response of benthic macroinvertebrates to gradients in hydrological connectivity : a comparison of temperate , subtropical , Mediterranean and semiarid river floodplains. Freshw. Biol. 59, 630–648. https://doi.org/10.1111/fwb.12292

Hawking, J.H., Smith, L.M., Busque, K.L., 2006. Identification and ecology of Australian freshwater invertebrates. www.mdfrc.org.au/bugguide

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

Hertz, J.T., Lyaruu, L.J., Ooi, E.E., Mosha, F.W., Crump, J.A., 2016. Distribution of Aedes mosquitoes in the Kilimanjaro Region of northern Tanzania. Pathog. Glob. Health 110, 108–112.

Javornik, C.J., Collinge, S.K., 2016. Influences of annual weather variability on vernal pool plant abundance and community composition. Aquat. Bot. 134, 61–67.

Jiang, Y., Xu, G., Xu, H., 2016. Use of multivariate dispersion to assess water quality based on species composition data. Environ. Sci. Pollut. Res. 23, 3267–3272.

Junk, K.., Wantzen, W.., 2004. The Flood Pulse Concept: New Aspects, Approaches and Applications-An Update, in: Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, Food and Agriculture Organization of the United Nations (FAO) and the Mekong River Commission (MRC). pp. 117–140.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989a. The Flood Pulse Concept in River-Floodplain Systems, in: Dodge, D.P. (Ed.), Proceedings of the International Large River Symposium (LARS). Canadian Special Publication of Fisheries and Aquatic Sciences 106. pp. 110–127.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989b. The Flood Pulse Concept in River-Floodplain Systems. Can. J. Fish. Aquat. Sci. 106, 110–127.

Kaaya, L.T., Day, J.A., Dallas, H.F., 2015. Tanzania River Scoring System (TARISS): a macroinvertebrate-based biotic index for rapid bioassessment of rivers. African J. Aquat. Sci. 40, 109–117.

Kiptala, J.K., Mohamed, Y., Mul, M.L., Cheema, M.J.M., Van Der Zaag, P., 2013. Land use and land cover classification using phenological variability from MODIS vegetation in the Upper Pangani River Basin , Eastern Africa. Phys. Chem. Earth 66, 112–122.

Kiptala, J.K., Mul, M.L., Mohamed, Y., Zaag, P. van der, 2013. Modelling stream flow and quantifying blue water using modified STREAM model in the Upper Pangani River Basin , Eastern Africa. Hydrol. Earth Syst. Sci. 10, 15771–15809.

Kling, L.J., Juliano, S.A., Yee, D.A., 2007. Larval mosquito communities in discarded vehicle tires in a forested and unforested site: detritus type, amount, and water nutrient differences. J. Vector Ecol. 32, 207–217.

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Glob. Ecol. Biogeogr. 23, 1324–1334.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Leibold, M.A., Chase, J.M., Ernest, S.K.M., 2016. Community Assembly and the Functioning of Ecosystems: How Metacommunity Processes Alter Ecosystems Attributes. Ecology 98, 909–919.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept : a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613.

Lumbreras, A., Marques, J.T., Belo, A.. ., Cristo, M., Fernandes, M., Galioto, D., Machado, M., Mira, A., Sá-Sousa, P., Silva, R., Sousa, L.., Pinto-Cruz, C., 2016. Assessing the conservation status of Mediterranean temporary ponds using biodiversity : a new tool for practitioners. Hydrobiologia 782, 187–199.

Mathew, M.M., Majule, A.E., Marchant, R., Sinclair, F., 2016. Variability of Soil Micronutrients Concentration along the Slopes of Mount Kilimanjaro , Tanzania. Appl. Environ. Soil Sci. 1–7.

Merritt, R.W., Cummins, K.W., 1996. An Introduction to the Aquatic Insects of North America, Third Edition. Kendal/Hunt Publishing Company, Dubuque, USA.

MillenniumEcosystemAssessment, 2005. Ecosystems and Human Well-Being: Wetlands and Water Synthesis. World Resources Institute, Washington, DC.

Murrell, E.G., Juliano, S.A., 2013. Predation resistance does not trade off with competitive ability in early-colonizing mosquitoes. Oecologia 173, 1033–1042.

Mwaijengo, G.N., Vanschoenwinkel, B., Dube, T., Nicholas, K., Brendonck, L., 2020. Seasonal variation in benthic macroinvertebrate assemblages and water quality in an Afrotropical river catchment, northeastern Tanzania. Limnologica 82, 1–12.

Nhiwatiwa, T., Brendonck, L., Dalu, T., 2017. Understanding factors structuring zooplankton and macroinvertebrate assemblages in ephemeral pans. Limnologica 64, 1–26.

Nhiwatiwa, T., Brendonck, L., Waterkeyn, A., Vanschoenwinkel, B., 2011. The importance of landscape and habitat properties in explaining instantaneous and long-term distributions of large branchiopods in subtropical temporary pans. Freshw. Biol. 56, 1992–2008.

Nhiwatiwa, T., Dalu, T., 2016. Seasonal variation in pans in relation to limno-chemistry , size , hydroperiod , and river connectivity in a semi-arid subtropical region. Phys. Chem. Earth 97, 37–45.

Nhiwatiwa, T., De Bie, T., Vervaeke, B., Barson, M., Stevens, M., Vanhove, M.P.M., Brendonck, L., 2009. Invertebrate communities in dry-season pools of a large subtropical river : patterns and processes. Hydrobiologia 630, 169–186.

Nicolet, P., Biggs, J., Fox, G., Hodson, M.J., Reynolds, C., Whitfield, M., Williams, P., 2004. The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. Biol. Conserv. 120, 261–278.

Oertli, B., Biggs, J., Cereghino, R., Grillas, P., Joly, P., Lachavanne, J.-B., 2005. Conservation and monitoring of pond biodiversity : introduction. Aquat. Conserv. Mar. Freshw. Ecosyetems 15, 535–540.

Oertli, B., Cereghino, R., Hull, A., Miracle, R., 2009. Pond conservation : from science to practice. Hydrobiologia 634, 1–9.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, H.M.H., Szoecs, E., Wagner, H., 2016. Vegan Community Ecology Package version 2.4-1.

PBWO/IUCN, 2007a. IUCN Water and Nature Initiative and Pangani Basin Water Board. River Health Assessment Final Report, Pangani River Basin Flow Assessment. Moshi, Tanzania.

PBWO/IUCN, 2007b. Pangani River System: State of the Basin Report 2007. Moshi, Tanzania.

Piscart, C., Moreteau, J., Beisel, J., 2005. Biodiversity and structure of macroinvertebrate communities along a small permanent salinity gradient (Meurthe River , France). Hydrobiologia 551, 227–236.

Pyke, C.R., 2005. Assessing Climate Change Impacts on Vernal Pool Ecosystems and Endemic Branchiopods. Ecosystems 8, 95–105.

R Core Team, ., 2014. R: a language and environment for statistical computing [WWW Document]. URL http://www.R- project.org/.

Ramsar, 2002. The Convention on Wetlands. Resolution VIII . 33 Guidance for identifying , sustainably managing , and designating temporary pools as Wetlands of International Importance.pp1-7.

Rhazi, L., Grillas, P., Saber, E.-R., Rhazi, M., Brendonck, L., Waterkeyn, A., 2012. Vegetation of Mediterranean temporary pools : a fading jewel? Hydrobiologia 689, 23–36.

Rhazi, L., Grillas, P., Toure, M.A., Ham, L.T., 2001. Impact of land use in catchment and human activities on water, sediment and vegetation of Mediterranean temporary pools. C.R. Acad. Sci. Paris 324, 165–177.

Roiz, D., Ruiz, S., Soriguer, R., Figuerola, J., 2015. Landscape Effects on the Presence, Abundance and Diversity of Mosquitoes in Mediterranean Wetlands. PLoS One 10, 1–17.

Rooney, R.C., Carli, C., Bayley, S.E., 2013. River Connectivity Affects Submerged and Floating Aquatic Vegetation in FloodplainWetlands. Wetlands 1–13.

Rosset, V., Lehmann, A., Oertli, B., 2010. Warmer and richer ? Predicting the impact of climate warming on species richness in small temperate waterbodies. Glob. Chang. Biol. 16, 2376–2387.

Scoones, I., 1991. Wetlands in Drylands : Key Resources for Agricultural and Pastoral Production in Africa. Ambio 20, 366–371.

Sheldon, F., Boulton, A.J., Puckridge, J.T., 2002. Conservation value of variable connectivity : aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river , Cooper Creek. Biol. Conserv. 103, 13–31.

Spencer, M., Blaustein, L., Schwartz, S.S., Cohen, J.E., 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools : relationships with habitat size and permanence. Ecol. Lett. 2, 157–166.

Stals, R., De Moor, I.J., 2007. Guides to the Freshwater Invertebrates of Southern Africa. Coleoptera. Report No. TT320/07: 1–263, Water Research Commission, South Africa.

Thomaz, S.M., Mauricio, L.B., Bozelli, R.L., 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia 579, 1–13.

Tockner, K., Pennetzdorfer, D., Reiner, N., Schiemer, F., Ward, J., 1999a. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river - floodplain system (Danube, Austria). Freshw. Biol. 41, 521–535.

Tockner, K., Schiemer, F., Baumgartner, C., Kum, G., Weigand, E., Zweimuller, I., Ward, J., 1999b. The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. Regul. riversResearch Manag. 15, 245–258.

Turner, K.R., Morse-Jones, S., Fisher, B., 2010. Ecosystem valuation: a sequential decision support system and quality assessment issues. Ann. N. Y. Acad. Sci. 1185, 79–101.

Tuytens, K., Vanschoenwinkel, B., Waterkeyn, A., Brendonck, L.U.C., 2014. Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. Freshw. Biol. 59, 955–968.

UNDP, 2014. Reducing Land Degradation on the Highlands of Kilimanjaro Region. Dar es Salaam, Tanzania.

Van den Broeck, M., 2016. Monitoring and conservation of Maediterranean temporary ponds. KU Leuven, Belgium.

Van den Broeck, M., Waterkeyn, A., Rhazi, L., Grillas, P., Brendonck, L., 2015. Assessing the ecological integrity of endorheic wetlands , with focus on Mediterranean temporary ponds. Ecol. Indic. 54, 1–11.

Vanschoenwinkel, B., De Vries, C., Seaman, M., Brendonck, L., 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. Oikos 116, 1255–1266.

Vanschoenwinkel, B., Hulsmans, A., De Roeck, E., De Vries, C., Seaman, M., Brendonck, L., 2009. Community structure in temporary freshwater pools : disentangling the effects of habitat size and hydroregime. Freshw. Biol. 54, 1487–1500.

Vonesh, J.R., Blaustein, L., 2010. Predator-induced shifts in mosquito oviposition site selection: A meta-analysis and implications for vector control. Isr. J. Ecol. Evol. 56, 123–139.

Waterkeyn, A., Grillas, P., Brendonck, L., 2016. Experimental test of the ecosystem impacts of the keystone predator Triops cancriformis (Branchiopoda: Notostraca) in temporary ponds. Freshw. Biol. 61, 1392–1404.

Waterkeyn, A., Grillas, P., Vanschoenwinkel, B., Brendonck, L., 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. Freshw. Biol. 53, 1808–1822.

Weilhoefer, C., Pan, Y., 2008. The effects of river floodwaters on floodplain wetland water quality and diatom assemblages. Wetlands 28, 473–486.

Williams, D.D., 2006. The biology of temporary waters. Oxford Biology, pp. 268.

Williams, D.D., 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. J. North Am. Benthol. Soc. 15, 634–650.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, D., 2003. Comparative biodiversity of rivers , streams , ditches and ponds in an agricultural landscape in Southern England. Biological 115, 329–341.

Zuur, A.K., Ieno, E.N., Smith, G.M., 2007. Analysing Ecological Data. Springer + Business Media,LLC,Sring Street, New York,NY 10013,USA.

Supplementary Information to Chapter 4

Table S1 Macroinvertebrates taxa occurrences (presence-absence) along the Ruvu River. Abbreviations: RV=Ruvu River, RD=Dehu River, RS=Soko River

Taxa		Monitoring sites													
		RV 1	RV 3	RV 5	RV 7	RV 8	RV 9	RV 10	RD 1	RD 3	RD 4	RD 5	RS 1	RS 3	RS 4
Ephemeroptera	Baetidae	+				+	+	+	+		+		+	+	+
	Caenidae				+	+	+	+	+	+	+		+	+	+
	Heptageniidae														
	Ephemerythidae														
	Leptophlebidae														
Trichoptera	Hydropsychidae						+								
	Ecnomidae				+			+							
	Leptoceridae														
	Philopotamidae														
	Hydroptilidae														
	Psychomiidae														
Odonata	Aeshinidae						+	+							
	Libellulidae				+		+				+		+		
	Gomphidae							+						+	
	Coenagrionidae	+			+	+	+	+		+	+		+	+	+
	Chlorocyphidae												+		
Annelida	Oligochaeta	+					+						+	+	+
	Hirudinea	+	+		+										
Gastropoda	Physidae									+					
	Lymnaenidae												+	+	+
	Planorbidae	+			+		+				+		+		
	Thiaridae					+				+	+	+	+	+	
Bivalvles	Sphaeriidae														
Trombidiformes	Hydrachnidiae														
Coleoptera	Gyrinidae														
	Elmidae					+					+		+		
	Psephenidae														
	Helodidae						+								
	Hydrophilidae	+			+	+	+	+							
	Torridincolidae						+								
	Noteridae	+			+										
	Curculionidae				+										
	Dytiscidae					+									
Crustacea	Potamonautidae								+	+	+				
	Atyidae					+					+				
Diptera	Athericidae														
	Tabanidae					+									
	Culicidae					+	+								
	Chironomidae	+	+	+	+	+	+	+		+	+	+	+	+	+
	Tipulidae												+		
	Simuliidae														
	Scyomyzidae					+							+		
	Dixidae														
	Psychodidae														
	Ceratopogonidae					+	+						+		
	Empididae														
	Stratiomyidae												+		
Hemiptera	Gerridae						+								
	Veliidae					+									
	Naucoridae	+			+	+	+	+			+				
	Mesoveliidae												+		
	Pleidae					+	+								
	Nepidae										+				
	Hebridae				+		+						+		
	Belostomatidae									+					
	Corixidae														
Lepidoptera	Pyralidae				+								+		
Araneae	Argyronetidae	+													
Porifera	Porifera														
Plecoptera	Notonemouridae														
	Perlidae														
Tricladida	Planaridae	+		+			+								+

Table S2 Ordination scores (coordinates on ordination axes) for each environmental variable

Environmental Variables	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Area (m^2)	0.1827	0.247117	0.7137	-0.076	-0.31779	-0.08919
Depth (cm)	-0.56315	0.527614	0.41427	-0.06544	-0.06959	0.20781
Temp (^{o}C)	0.29465	0.300111	0.41222	-0.17174	0.656829	0.06214
pH	0.75152	0.371471	-0.15723	-0.09817	-0.23163	-0.02731
EC (µS/cm)	-0.69239	-0.21778	0.35492	-0.26544	0.049159	-0.29282
DO (mg/L)	-0.56194	0.643666	-0.16851	-0.14615	0.118349	0.118
Turb (ftu)	0.61901	0.639464	-0.07546	0.05003	0.011225	0.03417
Chla (µg/L)	0.60453	0.538787	-0.09703	0.03261	0.06291	-0.22091
EmVeg (% cover)	-0.51368	0.59812	-0.40175	-0.04458	-0.1236	0.19008
SumVeg (% cover)	-0.69602	0.216104	0.41008	-0.13081	0.003218	-0.00991
NO_3^-(mg/L)	0.64387	0.323953	0.3329	-0.0747	-0.26602	-0.02592
NH4$^+$(mg/L)	0.55277	-0.36182	0.04218	-0.46003	0.003553	0.39408
TN (mg/L)	0.72165	-0.27913	0.13932	-0.11071	-0.06767	0.19552
TP (mg/L)	0.81429	-0.23782	0.26762	0.06263	0.0366	-0.01514
Fish	-0.83269	-0.16003	0.10532	-0.08175	-0.22343	0.13034
PondCon (m)	-0.08488	0.006992	0.384	0.78257	0.048193	0.22951

General Discussion

Although they occupy less than 1% of the earth’s land surface (Allen and Pavelsky, 2018), river ecosystems support a disproportionately large fraction of biological diversity (Allan and Flecker, 1993; Malmqvist and Rundle, 2002; Strayer and Dudgeon, 2010; Sinha et al., 2019) while, at the same time provide a plethora of services for humans including a source of water and food and a means of transportation, waste disposal and power production (Malmqvist and Rundle, 2002; Strayer and Dudgeon, 2010). Despite their importance, rivers are among the most threatened freshwater ecosystems on earth (Malmqvist and Rundle, 2002; Dudgeon et al., 2006; Strayer and Dudgeon, 2010;Vörösmarty et al., 2010). They are constantly threatened by habitat degradation, land-use change, pollution, flow modification, overexploitation, and climate change (Malmqvist and Rundle, 2002; Dudgeon et al., 2006; Perkins et al., 2010; Ledger and Milner, 2015). Nevertheless, a proper understanding of river ecosystem functioning and biological diversity is still lacking, especially in (sub) tropical regions. It was a key aim of this PhD study to investigate different factors that explain biodiversity and ecosystem quality in (afro) tropical river systems and associated temporary wetland ecosystems. By using macroinvertebrates as biological indicators and collecting environmental and biological data at various spatial-temporal scales, this work contributes to bridging the knowledge gap on factors controlling biodiversity, community structure and ecosystem functioning in (afro) tropical river ecosystems. Furthermore, this thesis has highlighted the importance of accounting for dendritic network structures and spatial autocorrelation in river systems; an important aspect which is often overlooked in riverine studies. This final chapter synthesizes the major findings of this thesis and its implications for both general ecology and river management. The chapter concludes by suggesting monitoring and conservation plans of these ecosystems, and directions for future research

Effect of seasonality on river ecosystem functioning

Distinct dry and wet seasonality produce dynamic flow regimes which regulate how tropical river systems function (Wantzen et al., 2006; Davies et al., 2008; Carrie et al., 2015). Poff et al. (1997) defined flow regime as “the master variable” for rivers, because it affects all instream variables including water quality, habitat availability, aquatic food webs, and the fluxes of essential carbon and nutrients, which in turn affect riverine community assemblages (Dallas, 2004; Douglas et al., 2005; Lewis, 2008). According to the River Wave Concept (RWC), the river flow is viewed as a series of waves changing through time which drive ecosystem processes and are responsible for the structure and organization of the physical form of the river and its floodplain (Humphries et al., 2014). It was one of the main aims of this thesis to provide a better understanding of how seasonality influences macroinvertebrate community structure and environmental conditions in afro-tropical river ecosystems (Chapters 1, 2 and 3) which are concurrently affected by increasing anthropogenic activities.

Across Chapters 1-2, our analyses provide evidence for presence of seasonal variation in riverine conditions in the UPRB. We showed that nutrient concentrations and turbidity levels increased significantly in the wet season, suggesting the strong effect of runoff carrying sediment and nutrient loads from the catchment area to the river systems during the rainy season (Kilonzo et al., 2014; Kalkhoff et al., 2016; Nhiwatiwa et al., 2017; Rostami et al., 2018). Seasonality in rainfall can indeed lead to shifts in hydrologic connectivity between constituent sources and receiving rivers and streams (Lintern et al., 2018). These findings will likely spur further research on seasonal changes in source, mobilization, and transport processes of sediments and nutrients from the catchment area to the river systems in the region.

In Chapters 1 and 2, we also showed that macroinvertebrate abundance and diversity decreased in the wet season. There are several possible explanations for these observations. First, increase in turbidity levels and nutrient concentrations in the wet season can have direct and indirect negative effect on macroinvertebrates, respectively. We checked this by carrying out correlation analysis between water quality variables and TARISS for the data of Chapter 1 and Chapter 2 combined. There is indeed a negative significant correlation between TARISS and nutrient variables and turbidity (Fig.1). High levels of suspended sediments can act to smother and scour habitats and biota hence limiting macroinvertebrate settling and colonization (Bilotta and Brazier, 2008). This suggests that the levels of streambed sedimentation can be one of the driving factors behind the seasonal macroinvertebrate community patterns in the UPRB. Second, some of the macroinvertebrates tend to drift either actively or passively in response to abiotic and biotic conditions. Increases in discharge in the wet season fuels passive macroinvertebrate drifting (Brittain and Eikeland, 1988; Gibbins et al., 2007; Naman et al., 2016). Accordingly, we found significant negative effects of water velocity on macroinvertebrate biotic indices (Chapter 1). Macroinvertebrates may also have actively drifted to escape from unfavorable abiotic conditions in the wet season. Lastly, it should also be noted that the seasonal differences in macroinvertebrate community composition can also be partly explained by the life cycle dynamics of studied organisms. Different taxa show differential success between seasons according to their life-history strategies such as reproduction, colonization and establishment abilities (Verberk et al., 2008; Blanchette and Pearson, 2013; Botwe et al., 2015; Westveer et al., 2018) as also discussed in Chapter 1.

Apart from changing flow regime and water quality, substrate type was an important factor structuring macroinvertebrates both in the dry and the wet seasons. Stone substratum supported a large number of benthic macroinvertebrate taxa compared to gravel/sand/mud substrate (Chapters 1 and 2). This is related to oxygen level, habitat stability and availability of diverse microhabitats that provide refuge from currents and predation, and food for herbivores and detritivores linked to stone substratum compared to the habitats with fine substrate (Brooks et al., 2005; Allan and Castillo, 2007; Pan et al., 2013; Jun et al., 2016). This was further reflected in our analysis where macroinvertebrate based biotic indices showed a positive correlation between dry and wet seasons (Fig.2) i.e., sites with high taxon richness in the dry season also had relative high taxon richness in the wet season, suggesting that substratum degradation can perturb the macroinvertebrate community even when water quality remains good (Li et al., 2012).

Even though we indicated that fluoride is a natural occurring pollution in the studied region (Chapters 1, 2 and 3), we didn’t find any clear pattern between macroinvertebrate assemblages and changes in fluoride concentrations in the two seasons. Comparable macroinvertebrate taxa were found in river sites with high and low fluoride concentrations. Future studies aiming at assessing the influence of fluoride on invertebrate community composition should experimentally test different ranges of fluoride concentrations while controlling other confounding factors which cannot be achieved in field studies.

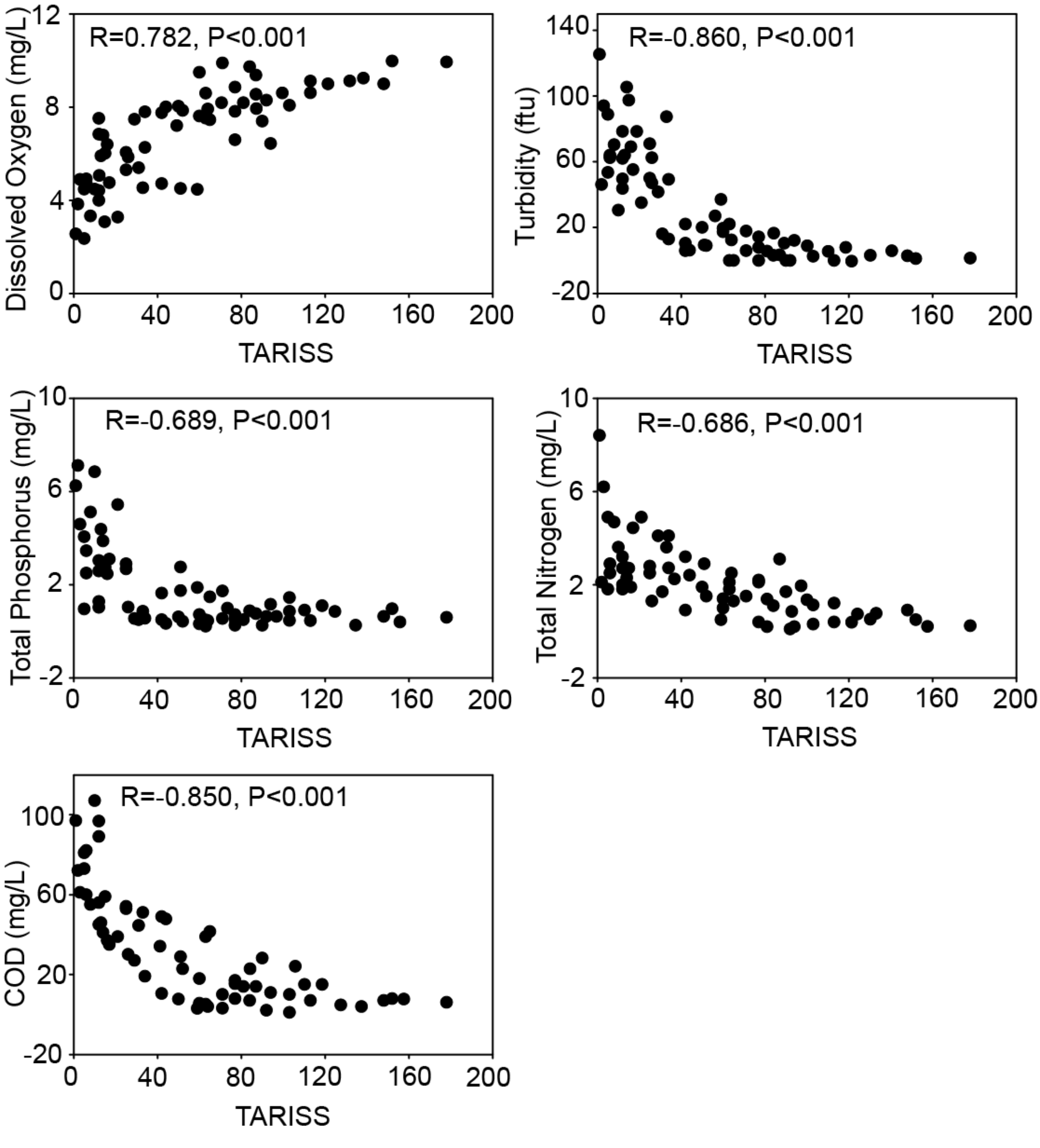

Fig.1. Spearman rank correlation between water quality variables and TARISS in the UPRB.

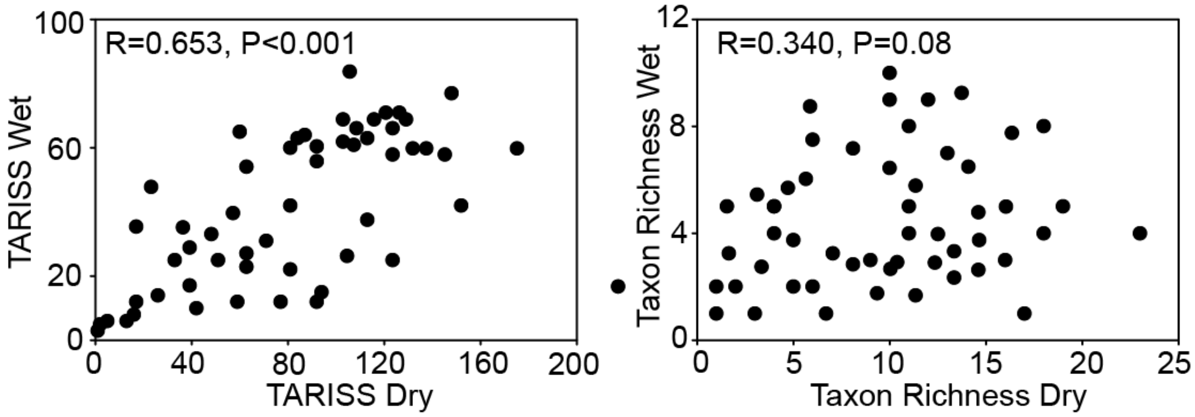

Fig.2. Spearman rank correlation for TARISS and Taxon Richness between dry and wet season in the UPRB.

We also examined whether macroinvertebrate functional feeding groups (FFGs) along the longitudinal river continuum in the Usa-Kikuletwa and Ruvu River catchments (Chapters 1 and 2) followed the predictions of the River Continuum Concept (RCC) (*sensu* Vannote et al., 1980) in the two seasons. The abundance and diversity of invertebrates FFGs is indeed one of the least understood attributes of Afro-tropical streams. We found that the FFGs did not completely match the RCC predictions along the longitudinal stream gradient. Based on the tenets of the RCC concept, Usa-Kikuletwa and Ruvu River catchments (both 1st to 4th order streams), would be expected to have equal numbers of shredders and collectors in the upper section of the river, followed by equivalent numbers of collectors and scrapers in the downstream sections (Vannote et al., 1980). The results based on percentage of taxa in FFGs, however, indicated a dominance of collectors (≥ 45%) at all sites followed by predators (Fig.3). The high abundance of collectors suggests an ample supply of fine particulate organic matter to support the large populations of collectors. While there was a minor seasonal variation in the FFGs of the benthic macroinvertebrate fauna (Fig.3), these results highlight some seasonality in the input and availability of organic matter in the rivers of the UPRB.

One notable characteristic of the studied river systems was the low representation of the shredders in all seasons, suggesting that shredder-mediated detritus processing does not prevail in the rivers of the UPRB. This could either be because of enhanced microbial activity replacing shredder activity at high temperatures, or be a result of low inputs and/or low palatability of detritus from dominant riparian trees in the region (Dobson et al., 2002). This is in accordance with previous studies who have demonstrated the lack of a cadre of shredders in East- African streams (Tumwesigye et al., 2000; Dobson et al., 2002; Masese et al., 2009). The main shredding taxa recorded in the UPRB are the freshwater crab *Potamonautes* spp. (Brachyura: Potamonautidae). Similar results were yielded in Kenya where freshwater crabs contributed to over 50% of the shredders in the headwater stream of the Mara River Basin (Masese, 2015).

Even though the data from this thesis (Chapters 1 and 2) contribute to the growing demand on the functional organization of Afro-tropical streams, the results should be interpreted with caution as the allocation of taxa to FFGs was based on information developed for temperate stream fauna (e.g., Merritt et al., 2008). Although the approach has been successful for some taxa, there is a growing body of evidence that related species occurring in different regions may sometimes not share the same diets (Dobson et al., 2002; Masese, 2015). Even within regions, some taxa can shift their feeding in response to changes in riparian conditions and land-use (Masese, 2015). This highlights the necessity for the development of keys and guides for Afro-tropical stream fauna aided by the analysis of gut contents in order to improve our understanding of the invertebrate functional organization of rivers and streams in the region.

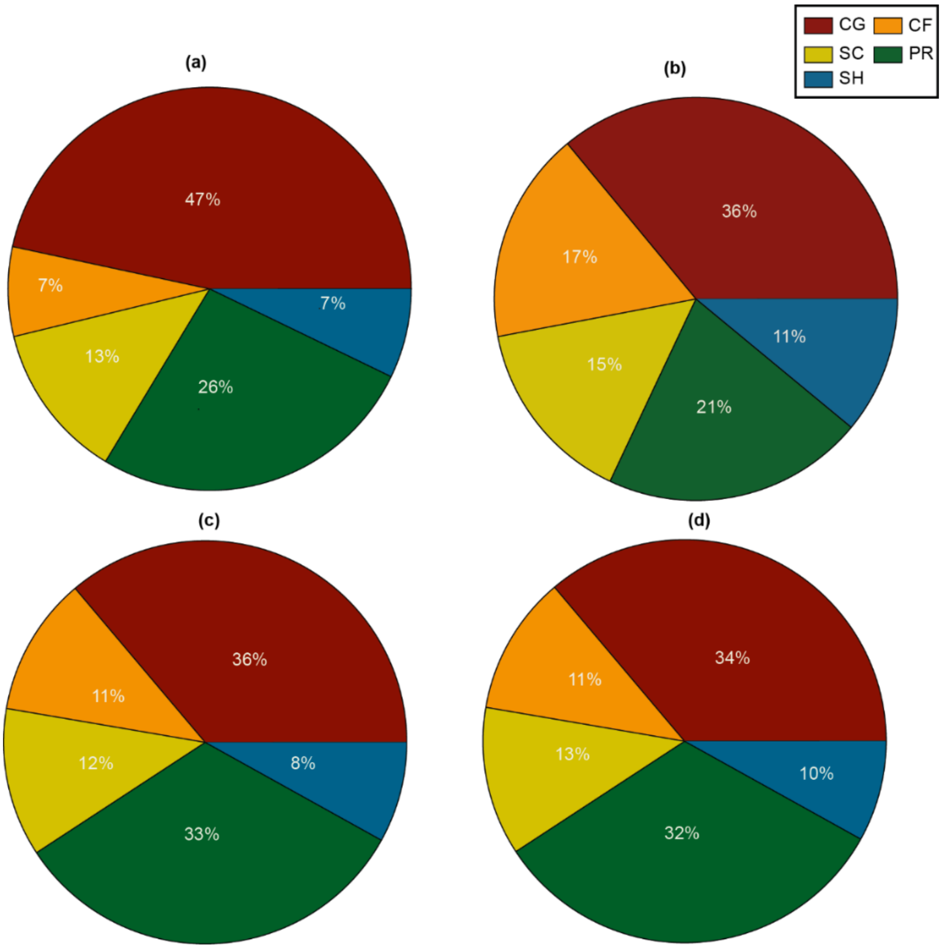

Fig.3. Percentage composition of macroinvertebrate functional feeding groups in Usa-kikuletwa (a, b) and Ruvu (c, d) River catchments, for the dry (a, c) and wet (b, d) seasons. CF= Collector filters, CG= Collector gathers, PR= Predators, SH= Shredders, and SC = Scrapers.

So far, we have focused on the biodiversity and ecosystem quality along the main river channel. The dynamic flow regime produced by alternating dry and wet seasons is an important factor in enhancing biodiversity and productivity in river-floodplain ecosystems, which has been integrated in the Flood Pulse Concept (FPC) (Junk et al., 1989a; Junk, 1999) and in the RWC (Humphries et al., 2014). The FPC describes the rivers and their associated floodplains as integrated components of a single dynamic system, linked by strong interactions between hydrological and ecological processes (Junk, 1999). The major driving force is the seasonal pulsing of river discharge that determines the degree of connectivity and the exchange processes of matter and organisms across river-floodplain gradients, thereby influencing the biodiversity and productivity of the entire river-floodplain ecosystem (Junk et al., 1989a; Ward and Stanford, 1995).

In chapter 4 we attempted to assess the role of seasonal river connections in modulating macroinvertebrate community structure in a set of temporary pools in the Ruvu River floodplain ecosystem. We showed that river connected pools were characterized by a dominance of riverine taxa e.g., mayflies *Baetis* sp., hydrophilid beetles *Berosus* sp., and atyid shrimps *Atyopsis* sp., and presence of fish such as tilapia and *Clarias* sp. These results are indicative of invertebrate and vertebrate dispersal from the river channel into the floodplain pools, which is in accordance with the predictions of FPC (Junk et al., 1989a; Junk, 1999). The presence of fish in the river connected pools structured the macroinvertebrate community assemblages through selective predation, particularly of large branchiopods. This finding supports similar studies which have demonstrated that the occurrence of large branchiopods in floodplain pools is limited by the predation effect of fish (Nhiwatiwa et al., 2011; Dube et al., 2019).

It was also shown that macroinvertebrate beta diversity (i.e., community dissimilarity between pools) was higher in river connected pools compared to endorheic ones (Chapter 4). Differences in hydrological connectivity and associated environmental conditions in river connected pools may have influenced community heterogeneity as a result of stochastic effects acting on the colonization process (Paillex., 2007; Gallardo et al., 2014; Larsen et al., 2019), consequently increasing beta diversity. In addition, variation in habitat characteristic between river connected and endorheic pools enhanced regional gamma diversity. Pools directly connected to the river were likely to be colonized by taxa with relatively low aerial dispersal ability (e.g., *Caridina* sp.) whereas endorheic ones were dominated by good dispersers (e.g., *Notonecta* sp.). The high regional (gamma) diversity has far-reaching benefits to the overall river-floodplain ecosystem functioning (e.g, enhanced nutrient cycling and ecosystems productivity, food chain support) and to the surrounding communities that depend on ecosystem services, including sources of food such as fish, derived by these vital ecosystems. As such, we propose maintaining both river connected and endorheic pools to promote overall a high regional biodiversity.

Besides differences in habitat types influenced by seasonal river connections, in Chapter 4 we also quantified key environmental factors that predominately influence variation in diversity and community composition of macroinvertebrates in temporary floodplain pools. We showed that macrophyte cover, average pool depth, presence of fish, and chlorophyll-a were key environmental factors underlying variation in macroinvertebrate diversity and community composition in the temporary pools. We found a positive relationship between macroinvertebrate taxon richness, macrophyte cover and pool depth (Chapter 4). Macrophytes are known to increase the diversity and abundance of aquatic invertebrates due to the habitat complexity they provide, which improves food availability and provides shelter against predators (Nicolet et al., 2004; Nhiwatiwa et al., 2017). A positive relationship between pool depth and macroinvertebrate taxon richness, confirms the importance of the duration of the aquatic phase (i.e., hydroperiod) as a determinant of community processes in temporary pools (Brooks and Hayashi, 2002; Waterkeyn et al., 2008; Vanschoenwinkel et al., 2009; Nhiwatiwa et al., 2011). This is because a longer hydroperiod tends to provide more opportunities for temporal niche segregation (Williams, 2006).

Important information with socio-economic relevance for the local communities is that the temporary floodplain pools in the Ruvu River catchment don’t hold mosquitoes (*Anopheles*, *Culex, Aedes*) which count as an ecosystem disservice as they can act as vectors for diseases such as Malaria and Dengue. Their absence suggests that temporary floodplain pools may not be a desirable habitat for these taxa, as frequently deemed by local communities. Instead, highly ephemeral aquatic habitats such as used tires, buckets and plastic bags have been reported to be a more suitable habitat for these taxa (Kling et al., 2007; Roiz et al., 2015; Hertz et al., 2016). We suggest maintaining temporary pools in the region because they provide a plethora of ecosystem services to the local communities including a source of water for domestic use, water storage for grazing and agriculture and a source of pasture for livestock. In addition, the pools constitute an educational source, even though its importance remains hardly valued. During the fieldwork, we tried to raise awareness of the potential benefits of temporary pools to the (curious) local people.

For the sustainable management of biodiversity and of freshwater ecosystems in the region, information from Chapter 4 contributes towards an inventory of aquatic invertebrates of the temporary floodplain pools. Before this study, there was an information gap on the diversity and community structure of aquatic invertebrates in temporary pools in the region. This study will likely spur further research in this topic and fuel the recognition of small waterbodies by local authorities responsible for management of water resources (e.g., Pangani Basin Water Office), inclusion of small waterbodies in the national water policy and streamlining the information into decision-making processes for effective biodiversity conservation and sustainable management of water resources in the region. This will further contribute to the national goal of achieving improved land and water resources management as stipulated in Tanzania Development Plan Vision 2025 (NDPV 2025) and realize the current National Biodiversity Strategy and Action Plan (NBSAP 2015-2020).

Anthropogenic influence on river quality at multiple spatial scales

Understanding the influence of anthropogenic activities on river quality has been a major focus of river monitoring programs worldwide (Allan, 2004; Mouri et al., 2011; Ambarita et al., 2016). It is widely accepted that rivers are the product of their catchments (Quinn et al., 1997), with strong ties between human activities and land-use types in the catchment which in turn influence the overall river quality. However, much of our understanding of the effects of land-use on streams and rivers is largely based on studies of temperate ecosystems and defining appropriate land-use spatial scales is not always straightforward and discrepancies exist in the literature.

In Chapters 1 and 2 we first assessed the influence of land use on water quality and macroinvertebrate assemblages. We found several significant relationships between land-use types and macroinvertebrate and water quality attributes (Chapters 1 and 2). We revealed that the macroinvertebrate based biotic index (TARISS) for water quality had a significant strong positive correlation with dense forest cover ($R=0.895$, $p < 0.001$), a positive correlation with agroforestry ($R= 0.463$, $p <0.001$), and a significant negative correlation with agriculture land-use ($R= -0.694$, $p < 0.001$) (Fig. 4). Similarly, in Chapter 2 we showed that turbidity levels and nutrient concentrations had a positive correlation with percentage irrigated mixed crops and a negative correlation with percentage Afromontane forest. These results suggest that agriculture is the main anthropogenic activity that affects the river ecosystem quality in the basin and that forests provide a buffer against anthropogenic impacts, in line with other studies in the wolrd (Ahearn et al., 2005; Rolls et al., 2012; Bu et al., 2014; Tudesque et al., 2014; Bere et al., 2016). From a management point of view, our results call upon the Pangani Basin Authority to enforce legal prohibition of human activities within 60 meters from a water source as stipulated in the national water policy (URT, 2002), in order to preserve the riparian forest which may help to alleviate some of the observed negative effects of agricultural activities (Chapters 1 and 2). This should also go in hand with controlled access to agricultural land in the river-floodplain ecosystems (Chapter 4). In addition, the local communities should be educated to conduct agroforestry (mixed forest and crop cultivation) where possible as it was established in the current study to also provide buffering against negative agricultural effects. Moreover, reforestation of degraded sections in the catchment using indigenous tree species will help to restore the integrity of river and streams. This should go in hand with provision of financial support and continued capacity building to local people through Community Based Forest Management (CBFM) associations.

It needs to be noted that the demand for agricultural land will continue to grow in the coming years to meet increasing food requirements and provide income for the growing human population. In addition, the government of Tanzania through the Ministry of Agriculture has also encouraged fertilizer application on farms by subsidizing fertilizers for farmers (Cameron et al., 2017). These changes will have implications for the functioning of the river through modifications in vegetation cover, run-off processes, erosion, and nutrient inputs. This highlights the need for further studies that examine management aspects of agriculture activities in the basin including fertilizer and pesticide use (i.e., types, amount, sources, handling, use frequency, application methods and timing, disposal of containers (pesticides)), and tillage practices. This will contribute to better assessment of agriculture influences on river quality and thus establish appropriate monitoring strategies and sustainable land-use management plans for the river basins in the region. While non-point sources of pollution are difficult to prevent, future adoption of best fertilizer and pesticide usage practices are needed to help improve water and soil conservation in the region.

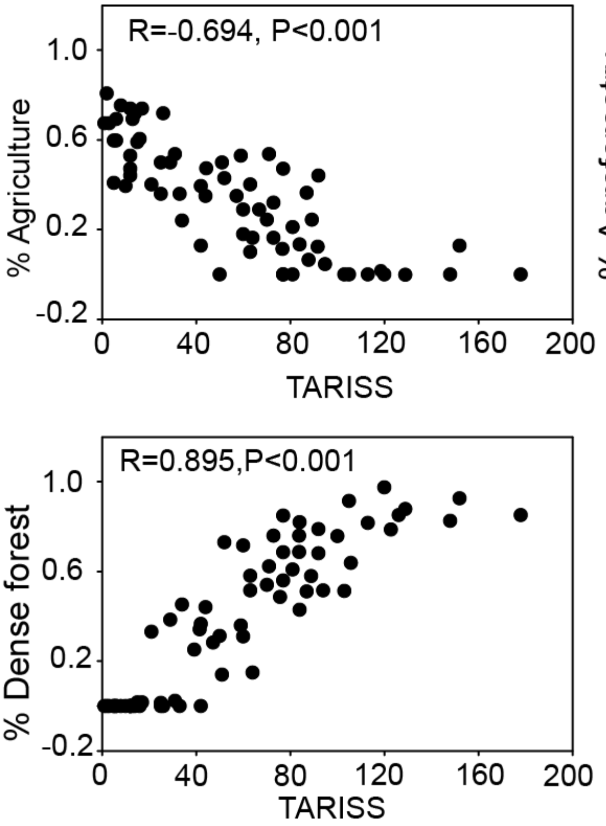

Fig.4. Spearman rank correlation between TARISS and percentage land-use types in the UPRB.

In order to define appropriate spatial scales for land-use, we secondly contrasted land-use effects on river quality at different spatial scales using three different spatial methods of land-use estimation: (i) land-use of the entire watershed area above the monitoring site, (ii) a circular buffer around a monitoring site, and (iii) a circular buffer immediately upstream of a monitoring site (Chapter 2). Circular buffers varied from 100m to 2km. We showed that physical-chemical water quality was highly related to features of land-use at the entire watershed scale while benthic macroinvertebrates were strongly influenced by land-use at a smaller spatial scale (e.g., 100 m). These results reveal that stream water quality conditions respond to cumulative anthropogenic, natural in-stream and/or allochthonous inputs (Tudesque et al., 2014), in line with the linear concept of nutrient enrichment along the stream gradient, from the upper to the lower reaches (i.e., river continuum, Vannote et al., 1980). Accordingly, macroinvertebrates may be more sensitive to local land-use disturbances than those occurring at broader spatial scales, as this is the template experienced directly by the organisms (Johnson et al., 2007; Dalu et al., 2017). Reach-scale (riparian) land-use, for example, determines allochthonous leaf litter inputs, composition and quality which in turn determine the macroinvertebrate functional organization (i.e., dominance of either shredders, scrappers or collectors) with effects on the processing of organic matter and the entire ecosystem functioning. Overall, our conclusion is that (i) water chemistry and macroinvertebrate assemblages respond differently to land-uses at different scale, (ii) different land-use metrics can indeed yield largely the same, but sometimes also unique information, (iii) and that the spatial estimate used and the spatial scale considered can strongly confound conclusions that can be drawn, (iv) suggesting that more regional studies are needed to improve our understanding and develop general paradigms on the multi-scale relationships between land-use and river quality. This is more so the case in Afrotropical rivers and streams which are underrepresented in global studies.

Apart from agricultural land-use activities, over-abstraction of water for irrigation purposes is another anthropogenic activity impacting the ecosystem function of river systems in the UPRB (Shaghude, 2006; Komakech and Zaag, 2011; Lalika et al., 2015b). Changes directly linked with the excessive abstraction of water are the modifications of streamflow in many parts of the UPRB, including the Kikuletwa River (PBWO/IUCN, 2007b) which have caused the river dis-continuum. In the dry season some rivers which used to be perennial are now non-perennial (PBWO/IUCN, 2007a; Mwaijengo *pers.obs.*), with stagnant pools remaining holding poor water quality with high temperature and ion concentrations (Mwaijengo *pers.obs.*). This has a negative effect on the ecological integrity of river systems resulting in significant losses of habitats and macroinvertebrate diversity (i.e., loss of specialized taxa and change from permanent towards the ephemeral river assemblages, with possible dominance by more opportunistic and a few hardy species), and health impacts to the local community who predominantly rely on river water for domestic purposes. Using the contaminated water increases the risk of exposure to enteric bacterial, protozoan, and viral pathogens that can cause diseases to the local community. A decrease in macroinvertebrate production and biodiversity has consequences for the management of native fisheries. In fact, changes in fish stocks due to reduction in water flow have been reported in Nyumba ya Mungu dam and the Kirua swamp (PBWO/IUCN, 2007b; Mwamila et al., 2008).

From a socio-economic point of view, sustainability of the ecosystem services from the UPRB is dependent on a systematic and improved water allocation for different uses (Komakech, 2013; Lalika et al., 2015a). The question, however, remains how much water should an upstream catchment area leave in the river for downstream users in order to sustain the ecosystem? There is no doubt, if we want to maintain watershed health and sustainable water flow, integrated water resources management approaches (i.e., existence of a coordinated development and management of water, land, and related resources) should be in place through the guidance of the Dublin Principles (Lalika et al., 2015b). This calls for scientifically defensible approaches to define environmental flows for the complex array of rivers in the UPRB. Sharing of ecological and hydrological knowledge among the scientific community in the region is also needed as extreme climate events are likely to lead to more water shortage and thus increasing ecosystem stress. More importantly we recommend: (i) water development and management should be based on a participatory approach, involving users, planners and policy makers at all levels (*sensu* Dublin Principles, 1992), (ii) more efficient use of rainfall through improved harvesting techniques, (iii) basin water bodies should make enforcement of legislation pertaining to water governance, (iv) future water policy review towards a more holistic and integrated water management system, and (v) as advocated by Lalika et al. (2015a) water management strategies and policies aiming at improving watershed conservation and ecosystem services should also focus on improving the welfare of the local communities, who are the primary beneficiaries of water from watersheds. In this way, we contribute to the realization of several of the 17 Sustainable Development Goals (SDGs) targets including improving water quality and access to safe and affordable water, biodiversity conservation, quality education, good health, and well-being.

Spatial autocorrelation in dendritic river networks

In Chapter 3 we added a main constraint that is not always included in studies of river systems: river network structure and spatial autocorrelation among sites. In Chapters 2 and 3 we indicated that rivers are hierarchically organized systems and that nested watersheds and flow connectivity may, therefore, produce spatial autocorrelation patterns among sampling sites (Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010). To explore the question on how dendritic river networks configure spatial autocorrelation in in-stream variables, in Chapter 3, we scrutinized the role of stream network structure in determining the spatial patterns of benthic macroinvertebrates and water chemistry at the catchment scale using the spatial stream network (SSN) models (Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010).

We revealed that spatial patterns and spatial autocorrelation exist in stream water chemistry (i.e., fluoride, total nitrogen, and total phosphorus) and macroinvertebrate indices (taxon richness and TARISS) comprising both flow-connected (tail-up) and flow-unconnected (tail-down) spatial relationships (Chapter 3). This corresponds with our findings in Chapter 2, where we described how processes occurring at multiple spatial scales often interact creating hierarchical correlated changes in water quality and community characteristics (Frissell et al., 1986; Allan et al., 1997; Tudesque et al., 2014; Dalu et al., 2017). We showed that water chemistry variables indicated flow-connected spatial dependence over a broad-scale, except for total nitrogen. This suggest that the unidirectional flow of water in river networks dictates how a downstream sites are influenced by upstream sites, and thus water chemistry attributes among sites may not be spatially independent (Gardner and Mcglynn, 2009). We also showed that fluoride levels exhibited spatial autocorrelation that included flow-unconnected relationship at broad-scale ranges, suggesting the effect of basin geology on stream water chemistry (Dent and Grimm, 1999; Mcguire et al., 2014; Chacha et al., 2018) whereby spatially distant sites may share similar water quality characteristics.

The existence of broad-scale tail-down, spatial relationships in the macroinvertebrates indices implies that most sites in the study area are to some degree related (Chapter 3). This was revealed by the relatively high similarity (low taxon turnover) among sites, suggesting that aquatic communities are strongly influenced by spatial processes occurring within and outside the river network. Most likely, the broad-scale relationship results from either macroinvertebrate movement: (a) in the stream itself (e.g., active or passive drifting, active benthic crawling (upstream or downstram), egg dispersal (drifting on the moving water)) (Lloyd et al., 2006; Bonada et al., 2012; Larsen et al., 2019), (b) out of the water but following the water course (e.g., aerial dispersal of insects), (c) and/or with water-associated vectors (e.g. waterfowl) (Rouquette et al., 2013), or the overriding landscape factors (geomorphology or bedrock geology) such that stream communities in a given segment may be just as similar to communities far up or downstream as they are to those in neighboring stretches (Poole, 2002). However, we have argued that correlation does not equal causation, therefore obtaining a full understanding of the underlying cause of spatial autocorrelation is not possible (Chapter 3). As such, the spatial structure in the models likely represents complex interactions between both in-stream and landscape factors and processes operating at multiple spatial scales (Richards et al., 1997; Bonada et al., 2012; Frieden et al., 2014).

From a practical and management point of view, SSN models are important as they can be used to make catchment-wide predictions of stream attributes while allowing stream network interactions to be inferred, due to the inclusion of a spatial autocovariance function (Ver Hoef et al., 2006). This was proven in our study whereby the models made good predictions of water chemistry and macroinvertebrate indices (Fig.5, Chapter 3). As such, we recommended SSN models to be used to support river basin management in the region because inferences about regional river conditions can be generated, and thus can be used to locate potentially impaired river segments in a rapid and cost-effective way (Chapter 3). However, the power of SNN models needs to be verified and validated in different river systems in the region before its full implementation.

Biological indicators of river ecosystem quality

Information on the community composition and diversity of aquatic macroinvertebrates can be used to assess the status and ecological integrity of rivers and associated floodplain wetlands (Rosenberg and Resh, 1993; Boix et al., 2005; Kaaya et al., 2015; Van den Broeck et al., 2015b). An initial step in assessing and monitoring ecological condition is therefore to conduct an extensive sampling survey from which reliable indicators could be detected (Oertli et al., 2010; Kaaya, 2014; Van den Broeck, 2016).

Information from all Chapters (1, 2, 3 and 4) of this thesis was part of an extensive sampling survey of macroinvertebrates from the river systems (Usa- Kikuletwa and Ruvu) and temporary floodplain pools (in Ruvu catchment) in the UPRB. We performed indicator taxa analysis to identify macroinvertebrate indicator taxa for the different water quality conditions in the river systems (Chapters 1) and for the two habitat types of the temporary floodplain pools (Chapter 4) of which the results are summarized in Table 1.

In Chapter 1, we showed that different sets of indicator taxa for water quality emerged in different seasons. The families Baetidae (Ephemeroptera) and Heptageniidae (Ephemeroptera) were shown to be indicator taxa of good water quality conditions in both seasons (Chapter 1). It was also revealed that the families Heptageniidae and Perlidae (Trichoptera) acted as good bioindicators of siltation and indirect effect of low oxygen levels, as these taxa showed a negative relationship with Sand/Mud (GSM) substratum (Chapters 1 and 2). Several members of the orders Ephemeroptera, Plecoptera, and Trichoptera are known to be sensitive to pollution (Rosenberg and Resh, 1993; Barbour et al., 1999; Soininen and Kononen, 2004), therefore, their presence is often an indication of good water quality condition (Rosenberg and Resh 1993; Barbour et al., 1999; Soininen and Kononen, 2004; Al-shami et al. 2011; Nhiwatiwa et al., 2017), comparable to the findings of our study.

The appearance of the family Potamonautidae as an indicator of good water quality in the dry season may be linked to it functional feeding characteristics and availability of food resources. As shown in the previous section, the main shredding taxa recorded in the UPRB are the freshwater crab *Potamonautes* spp., which are largely restricted to forested and well vegetated river sites. Their appearance may indicate that the amount, timing and quality of leaf litter input to the streams is more significant in the dry than in the wet season. On the other hand, sediment dwelling Chironomidae (Diptera) were an indicator of poor water quality conditions in the wet season. Larvae of most chironomid species are quite tolerant of low levels of dissolved oxygen and high levels of nutrients and turbidity (Marques et al., 1999; Al-shami et al., 2010; Özkan et al., 2010; Beneberu et al., 2014). Accordingly, they appeared as indicator taxa of poor water quality condition in the wet season when nutrients and turbidity were often problematic (Chapter 1). The current identified indicator taxa may, therefore, be used in future to monitor changes in ecological conditions of the studied river systems.

Table 1 List of indicator taxa and their corresponding indicator values for river and temporary pool ecosystems in the UPRB.

Aquatic systems	Water Quality/Pool type	Indicator taxa	Indicator Value
River	Good	Baetidae	0.929
		Hydropsychidae	0.886
		Heptageniidae	0.845
	Poor	Chironomidae	0.928
		Hydrophilidae	0.667
Temporary pools	River connected	*Baetis* sp.	0.775
	Endorheic	*Lestes* sp.	0.988
		S. wirminghausi	0.911
		Pseudagrion sp.	0.872

In Chapter 4 we showed that *Baetis* sp. appeared to be an indicator taxon for river connected pools, while *Lestes* sp., *Streptocephalus wirminghausi* and *Pseudagrion* sp. stood out as indicator taxa for endorheic pools. The finding of large branchiopods (i.e., *S. wirminghausi*) as indicators of endorheic pools supports their flagship status for temporary pool habitats (Brendonck et al., 2008; Van den Broeck, 2016). Large branchiopods can serve as indicators of good conservation status of temporary pools (Lumbreras et al., 2016; Dube et al., 2020), nevertheless are capable of surviving in disturbed environments that are characterized by high turbidity levels, high total phosphate concentrations (Thiery, 1991; Waterkeyn et al., 2009; Van den Broeck et al., 2015a), intensive grazing and shortened hydroperiods (Van den Broeck et al., 2015a, 2019). Although we have made a significant contribution to the growing data on indictor taxa of temporary freshwater ecosystem in the region, future multiple sampling surveys are needed to discover more invertebrate taxa linked to different hydrological connectivity and environmental conditions in temporary floodplain habitats (Nhiwatiwa et al., 2011; Torres et al., 2018; Dube et al., 2019).

In Chapters 1, 2 and 3 we also computed a biotic index based on aquatic macroinvertebrates (i.e., Tanzania River Scoring System (TARISS)) as an indicator of water pollution and the general disturbance in river condition. We showed that TARISS was able to distinguish between dry and wet seasons, and upstream sites from agricultural impacted downstream ones (Chapters 1 and 2), thus providing a good indication of the variable ecological conditions of the river systems between sites and seasons. For future monitoring programmes of river systems in the country, the TARISS index offers a reliable, cost-effective, yet scientifically valid tool. Nevertheless, to ensure its reliable large-scale applicability, the index needs to be tested on a larger geographical scale (i.e., across different geographical regions and climatic conditions in the country) before it can be integrated into a variety of policy and regulatory mechanisms. By doing so, more indicator taxa may potentially be discovered in other river systems, disparities among the regions compared, and sensitivity scores adapted, thus resulting in an improved bioassessment system. In the UPRB, for example, the sensitivity score for the family Potamonautidae needs adjustment because it appeared to be an indicator taxon of good water quality conditions, while in TARISS it is rated as a pollution tolerant taxon. There is also a need for more work to strengthen TARISS by improving its ability to reflect other forms of pollution such as heavy metal and pesticide pollutions, besides organic pollution and eutrophication.

In addition, since landscape factors appeared to influence macroinvertebrate community similarity even at distant flow-unconnected sites, multivariate biomonitoring approaches such as the River Invertebrate Prediction and Classification System (RIVPACS) of the United Kingdom (Wright et al., 1984) and the AUStralian RIVer Assessment Scheme (AUSRIVAS) (Davies, 2000) can be adopted and tested in Tanzanian river systems to supplement the information provided by TARISS. These models integrate the predictive power of landscape features such as slope, altitude, and stream order in assessing the biological river health and hence predict the aquatic macroinvertebrate fauna expected to occur at a site (and from each habitat type including riffle, edge, pool and bed habitats) in the absence of environmental stress, such as pollution or habitat degradation, to which the fauna collected at a site can be compared.

Overall, the results from this study highlight usefulness of biomonitoring programs in assessing river ecosystem health, even at coarse taxonomic resolution such as family-level as used in this study. Results yield robust relationships between environmental conditions and ecological responses. However, the current national water policy (URT, 2002) and the guideline for water resources monitoring and pollution control (URT, 2012) do not recognize the use of biological indicators in assessment of ecological conditions of aquatic systems. We, therefore, recommend the inclusion of different organism groups (such as periphyton, benthic macroinvertebrates, fish, and macrophytes) to be used either singly or together, in the assessment of ecological conditions of inland waters in Tanzania. This may reduce the cost of performing water chemical analyses which is often prohibitively high, thus limiting regular monitoring of river quality.

Climate change impact on river and wetland ecosystems

Climate change is another factor that has the potential to cause negative impacts on river and wetland ecosystems in the region (PWBO/IUCN, 2010; Munishi and Sawere, 2014; Lalika et al., 2015b; Kishiwa et al., 2018). Although we did not factor it in our analysis, there is increasing evidence that climate change will intensify the already perceived negative human impacts. One of the most prevalent and potentially devastating impacts of climate change in the region is the change in temperature and rainfall intensity, frequency, and predictability (WWF, 2006; PWBO/IUCN, 2010; Adhikari et al., 2015). The climate change projections suggest that East Africa will experience warmer temperatures (rise in temperature ranging from 1.4°C to 5.5°C) and an increase in rainfall from December to February by 5-20% and a 5-10% decrease in rainfall from June to August by 2090s (WWF, 2006; IPCC, 2007; Adhikari et al., 2015). However, these changes may not be uniform throughout the year, and may likely occur in sporadic and unpredictable events (IPCC, 2007; PWBO/IUCN, 2010; Adhikari et al., 2015).

Increased precipitation, especially heavy rainfall, may create flooding that increases sediment loads and raises the levels of nutrient and chemical pollution in surface water from agricultural land, industries, and sanitation facilities, thus affecting the overall water quality and macroinvertebrate community composition (Chapters 1, 2 and 4). It may also be likely that the increased precipitation will come in a few very large rainstorms thereby allowing river peak flows of short duration, thus negatively affecting river-floodplain hydrological connectivity, pool hydroperiod, community composition, and the overall functioning of river-floodplain ecosystems (Chapter 4). In addition, the projected reduced precipitation in the already dry season may cause severe droughts thus altering streamflow patterns, longitudinal river connectivity, and subsequently the availability of habitats for riverine biota (Chapter 1 and 3). Furthermore, warmer temperatures can have important consequences for the embryonic development, larval growth, metabolism and the overall survivorship of aquatic organisms (Lessard and Hayes, 2003; Haidekker and Hering, 2008; Li et al., 2009).

As a result, predicted changes will have profound effects on the overall functioning of river ecosystems and for the growing human population that is predominantly reliant on river ecosystem services such as water supply (for domestic, industrial and irrigation purposes) and food sources (e.g., fishes). We urge the local environmental management authorities, including the Pangani Basin Water Board, to factor in climate change (reflecting best possible scenarios of the future climate) when planning future water and land-use developments at all levels, in order to reduce environmental problems in the future. We also recommend long term and multiple monitoring surveys to provide the most comprehensive scientific information on the effects of intra and inter annual variation in climate conditions on riverine community composition and the river ecosystems at large (Hill et al., 2016). This will allow the formulation of appropriate environmental policy and management plans.

Finally, we do hope that our results will contribute to a sustainable management and conservation of freshwater habitats in the region in the short and long-term.

Scope for future work

Future work of monitoring, conservation, and management of river and wetland ecosystems in the UPRB can focus on different aspects. First, a further insight on the effect of seasonal variation in river condition can be gained by constructing models that predict how future scenarios of changes in rainfall patterns and temperature will impact stream hydrology and the river ecosystem structure and functioning. Second, given that the agricultural activities are bound to increase due to increased food demand following the population growth (National Bureau of Statistics, 2013), future research should make effort to quantify the effects of agriculture management practices on river ecosystem quality specifically focusing on amount and type of fertilizer and pesticide use, use frequency, application methods and timing at different spatial scale and using different sets of bioindicators. Third, studies should be promoted on macroinvertebrate dietary composition and requirements, and the ratios of functional feeding groups as surrogates of ecosystem attributes and functional indicators of river ecological health in the region. Fourth, as lotic systems are continued to be fragmented in the region, studies on dry-season river pools are needed in order to understand the patterns and ecological processes influencing invertebrate communities. This should also include contrast studies on community composition between dry-season river pools and other temporary pools so as to generate ecological paradigms. Lastly, as relatively powerful tools for the assessment of spatial patterns in stream characteristics over larger-scale, future works on verification and validation of the power of the SNN model in different river basins in the region are needed before its full operation**.**

References

Adhikari, U., Nejadhashemi, P.A., Woznicki, S.A., 2015. Climate change and eastern Africa : a review of impact on major crops. Food Energy Secur. 4, 110–132.

Ahearn, D.S., Sheibley, R.W., Dahlgren, R.A., Anderson, M., Johnson, J., Tate, K.W., 2005. Land use and land cover influence on water quality in the last free-flowing river draining the western Sierra Nevada , California. J. Hydrol. 313, 234–247.

Akoto, O., Adiyiah, J., 2008. Dissolved nitrogen in drinking water resources of farming communities in Ghana. African J. Environ. Sci. Technol. 2, 31–35.

Al-badaii, F., Shuhaimi-othman, M., Gasim, M.B., 2013. Water Quality Assessment of the Semenyih River ,Selangor,Malaysia. J. Chem.

Allan, D.J., Erickson, D.L., Fay, J., 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshw. Biol. 37, 149–161.

Allan, J.D., 2004. Landscapes and Riverscapes : The Influence of Land Use on Stream Ecosystems. Annu.Rev.Ecol.Syst 35, 257–84.

Allan, J.D., Flecker, A.S., 1993. Biodiversity Conservation in Running Waters Identifying the major factors that threaten destruction of. Bioscience 43, 32–43.

Allen, G.H., Pavelsky, T.M., 2018. Global extent of rivers and streams. Science (80-.). 361, 585–588.

Al-shami, S.A., Md Rawi, C.S., HassanAhmad, A., Nor, A.S.M., 2010. Distribution of Chironomidae (Insecta : Diptera) in polluted rivers of the Juru River Basin , Penang , Malaysia. J. Environ. Sci. 22, 1718–1727.

Al-shami, S.A., Rawi, C.S., Ahmad, A.H., Hamid, S.A., Nor, S.M., 2011. Influence of agricultural, industrial , and anthropogenic stresses on the distribution and diversity of macroinvertebrates in Juru River Basin ,Penang,Malaysia. Ecotoxicol. Environ. Saf. 74, 1195–1202. h

Ambarita, M.N.D., Lock, K., Boets, P., Everaert, G., Hanh, T., Nguyen, T., Anne, M., Forio, E., Liz, P., Musonge, S., Suhareva, N., Bennetsen, E., Landuyt, D., Dominguez-granda, L., Goethals, P.L.M., 2016. Ecological water quality analysis of the Guayas river basin (Ecuador) based on macroinvertebrates indices. Limnologica 57.

Azrina, M.Z., Yap, C.K., Ismail, A.R., Ismail, A., Tan, S.G., 2006. Anthropogenic impacts on the distribution and biodiversity of benthic macroinvertebrates and water quality of the Langat River, Peninsular Malaysia. Ecotoxicol. Environ. Saf. 64, 337–347.

Bagalwa, M., 2006. The impact of land use on water quality of the Lwiro River, Democratic Republic of Congo, Central Africa. African J. Aquat. Sci. 31, 137–143.

Beneberu, G., Mengistou, S., Eggermont, H., Verschuren, D., 2014. Chironomid distribution along a pollution gradient in Ethiopian rivers , and their potential for biological water quality monitoring. African J. Aquat. Sci. 39, 45–56.

Beyene, A., Addis, T., Kifle, D., Legesse, W., Kloos, H., Triest, L., 2009. Comparative study of diatoms and macroinvertebrates as indicators of severe water pollution: Case study of the Kebena and Akaki rivers in Addis Ababa, Ethiopia. Ecol. Indic. 9, 381–392.

Bilotta, G.S., Brazier, R.E., 2008. Understanding the influence of suspended solids on water quality and aquatic biota. Water Res. 42, 2849–2861.

Blanchette, M.L., Pearson, R.G., 2013. Dynamics of habitats and macroinvertebrate assemblages in rivers of the Australian dry tropics. Freshw. B 58, 742–757.

Boix, D., Gascon, S., Sala, J., Martinoy, M., Gifre, J., Quintana, X.D., 2005. A new index of water quality assessment in Mediterranean wetlands based on crustacean and insect assemblages : the case of Catalunya (NE Iberian peninsula). Aquat. Conserv. Mar. Freshw. Ecosyetems 15, 635–651.

Bonada, N., Doledec, S., Statzner, B., 2012. Spatial autocorrelation patterns of stream invertebrates : exogenous and endogenous factors. J. Biogeogr. 39, 56–68.

Botwe, P.K., Barmuta, L.A., Magierowski, R., McEvoy, P., Goonan, P., Carver, S., 2015. Temporal Patterns and Environmental Correlates of Macroinvertebrate Communities in Temporary Streams. PLoS One 1–19.

Brendonck, L., Rogers, C.D., Olesen, J., Weeks, S., Hoeh, W.R., 2008. Global diversity of large branchiopods (Crustacea : Branchiopoda) in freshwater. Hydrobiologia 595, 167–176.

Brittain, J.E., Eikeland, T.J., 1988. Invertebrate drift - A review. Hydrobiologia 166, 77–93.

Brooks, R.T., Hayashi, M., 2002. Depth-Area-Volume and Hdroperiod Relationships of Ephemeral (Vernal) Forest Pools in Southern New England. Wetlands 22, 247–255.

Bu, H., Meng, W., Zhang, Y., Wan, J., 2014. Relationships between land use patterns and water quality in the Taizi River basin , China. Ecol. Indic. 41, 187–197.

Calijuri, M., Cunha, D., Queiroz, L., Moccellin, J., Miwa, A., 2008. Nutrients and chlorophyll- a concentrations in tropical rivers of Ribeira de Iguape Basin, SP, Brazil. Acta Limnol. Bras. 20, 131–138.

Chuman, T., Hruška, J., Oulehle, F., Gürtlerová, P., Majer, V., 2013. Does stream water chemistry reflect watershedcharacteristics? Environ. Monit. Assess. 185, 5683–5701.

Dallas, H.F., 2004. Seasonal variability of macroinvertebrate assemblages in two regions of South Africa : implications for aquatic bioassessment. African J. Aquat. Sci. 29, 173–184.

Dalu, T., Wasserman, R.J., Tonkin, J.D., Alexander, M.E., Dalu, M.T.B., Motitsoe, S.N., Manungo, K.I., Bepe, O., Dube, T., 2017. Assessing drivers of benthic macroinvertebrate community structure in African highland streams : An exploration using multivariate analysis. Sci. Total Environ. 601-602, 1340–1348.

Davies, P.., 2000. Development of a national bioassessment system (AUSRIVAS) in Australia, in: Wright JF, Sutcliffe DW and Furse MT (eds.), Assessing the Biological Quality of Freshwaters. RIVPACS and Other Techniques. Freshwater Biological Association, Ambleside. pp. 113–124.

Davies, P.M., Bunn, S.E., Hamilton, S.K., 2008. Primary Production in Tropical Streams and Rivers, in: Tropical Stream Ecology. pp. 23–42.

Dobson, M., Magana, A., Mathooko, J.M., Ndegwa, F.K., 2002. Detritivores in Kenyan highland streams : more evidence for the paucity of shredders in the tropics ? Freshw. Biol. 47, 909–919.

Douglas, M.M., Bunn, S.E., Davies, P.M., 2005. River and wetland food webs in Australia ' s wet – dry tropics : general principles and implications for management. Mar. Freshw. Res. 56, 329–342.

Dube, T., de Necker, L., Wepener, V., Smit, N.J., Pinceel, T., Mwaijengo, G.N., Brendonck, L., 2020. A comparison of aquatic macroinvertebrate and large branchiopod community composition between temporary pans of a conservation area and surrounding communal area in South Africa. African Zool. 55, 1–11.

Dube, T., Pinceel, T., Necker, L. De, Wepener, V., Lemmens, P., Brendonck, L., 2019. Lateral hydrological connectivity differentially affects the community characteristics of multiple groups of aquatic invertebrates in tropical wetland pans in South Africa. Freshw. Biol. 1–15.

Dudgeon, D., 2010. Prospects for sustaining freshwater biodiversity in the 21st century : linking ecosystem structure and function. Curr. Opin. Environ. Sustain. 2, 422–430.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z., Naiman, R.J., Knowler, D.J., Leveque, C., Soto, D., Prieur-Richard, A.-H., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity : importance , threats , status and conservation challenges. Biol. Rev. 81, 163–182.

Frieden, J.C., Peterson, E.E., Webb, J.A., Negus, P.M., 2014. Improving the predictive power of spatial statistical models of stream macroinvertebrates using weighted autocovariance functions. Environ. Model. Softw. 60, 320–330.

Frissell, C.A., Liss, W.J., Warren, C.E., Hurley, M.D., 1986. A Hierarchical Framework for Stream Habitat Classification : Viewing Streams in a Watershed Context. Environ. Manage. 10, 199–214.

Gardner, K.K., Mcglynn, B.L., 2009. Seasonality in spatial variability and influence of land use / land cover and watershed characteristics on stream water nitrate concentrations in a developing watershed in the Rocky Mountain West. Water Resorces Res. Res. 45, 1–14.

Gibbins, C., Vericat, D., Batalla, R.J., Gomez, C.M., 2007. Shaking and moving : low rates of sediment transport trigger mass drift of stream invertebrates. Can. J. Fish. Aquat. Sci. 64, 1–5.

Haidekker, A., Hering, D., 2008. Relationship between benthic insects (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in Germany : A multivariate study. Aquat. Ecol. 42, 463–481.

Harding, J.S., Young, R.G., Hayes, J.W., Shearer, K.A., Stark, J.D., 1999. Changes in Agricultural Intensity and River Health Along a River Continuum. Freshw. Biol. 42, 345–357.

Hering, D., Johnson, R.K., Kramm, S., Schmutz, S., Szoszkiewicz, K., Verdonschot, P.F.M., 2006. Assessment of European streams with diatoms , macrophytes , macroinvertebrates and fish : a comparative metric-based analysis of organism response to stress. Freshw. Biol. 51, 1757–1785.

Hertz, J.T., Lyaruu, L.J., Ooi, E.E., Mosha, F.W., Crump, J.A., 2016. Distribution of Aedes mosquitoes in the Kilimanjaro Region of northern Tanzania. Pathog. Glob. Health 110, 108–112.

Hill, M.J., Sayer, C.D., Wood, P.J., 2016. When is the best time to sample aquatic macroinvertebrates in ponds for biodiversity assessment ? Environ. Monit. Assess. 188, 1–11.

Hrodey, P.J., Sutton, T.M., Frimpong, E.A., 2009. Land-Use Impacts on Watershed Health and Integrity in Indiana Warmwater Streams. Am. Midl. Nat. 16, 76–95.

Humphries, P., Keckeis, H., Finlayson, B., 2014. The River Wave Concept : Integrating River Ecosystem Models. Bioscience 64, 870–882.

IPCC, 2014. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Fifth Assessment.

IPCC, 2007. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Fourth Assessment Report, R.K. Pachauri & A. Reisinger, pp. 104.

Johnson, R.K., Furse, M.T., Hering, D., Sandin, L., 2007. Ecological relationships between stream communities and spatial scale : implications for designing catchment- level monitoring programmes. Freshw. Biol. 52, 939–958.

Junk, W.J., 1999. The flood pulse concept of large rivers : learning from the tropics. Large Rivers 11, 261–280.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989a. The Flood Pulse Concept in River-Floodplain Systems, in: Dodge, D.P. (Ed.), Proceedings of the International Large River Symposium (LARS). Canadian Special Publication of Fisheries and Aquatic Sciences 106. pp. 110–127.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989b. The Flood Pulse Concept in River-Floodplain Systems. Can. J. Fish. Aquat. Sci. 106, 110–127.

Kaaya, L.T., 2014. Biological Assessment of Tropical Riverine Systems Using Aquatic Macroinvertebrates in Tanzania, East Africa. University of Cape Town, South Africa.

Kaaya, L.T., Day, J.A., Dallas, H.F., 2015. Tanzania River Scoring System (TARISS): a macroinvertebrate-based biotic index for rapid bioassessment of rivers. African J. Aquat. Sci. 40, 109–117.

Kalkhoff, S.J., Hubbard, L.E., Tomer, M.D., James, D.E., 2016. Effect of variable annual precipitation and nutrient input on nitrogen and phosphorus transport from two Midwestern agricultural watersheds. Sci. Total Environ. 559, 53–62.

Kilonzo, F., Masese, F.O., Van Griensven, A., Bauwens, W., Obando, J., Lens, P.N.L., 2014. Spatial-temporal variability in water quality and macro-invertebrate assemblages in the Upper Mara River basin, Kenya. Phys. Chem. Earth 67-69, 93–104.

Kishiwa, P., Nobert, J., Kongo, V., Ndomba, P., 2018. Assessment of impacts of climate change on surface water availability using coupled SWAT and WEAP models : case of upper Pangani River Basin, Tanzania. Int. Assoc. Hydrol. Sci. 378, 23–27.

Kitalika, A.J., Machunda, R.L., Komakech, H.C., Njau, K.N., 2018. Land-Use and Land Cover Changes on the Slopes of Mount Meru-Tanzania. Curr. World Environ. 13, 331–352.

Kling, L.J., Juliano, S.A., Yee, D.A., 2007. Larval mosquito communities in discarded vehicle tires in a forested and unforested site: detritus type, amount, and water nutrient differences. J. Vector Ecol. 32, 207–217.

Komakech, H.C., 2013. Emergence and Evolution of Endogenous Water Institutions in an African River Basin: Local Water Governance and State Intervention in the Pangani River Basin, Tanzania. IHE Delft University of Technology.

Komakech, H.C., Zaag, P. Van Der, 2011. Understanding the Emergence and Functioning of River Committees in a Catchment of the Pangani Basin , Tanzania. Water Altern. 4, 197–222.

Lalika, M.C.S., Meire, P., Ngaga, Y.M., 2015a. Exploring watershed conservation and water governance along Pangani River Basin, Tanzania. Land use policy 48, 351–361.

Lalika, M.C.S., Meire, P., Ngaga, Y.M., Chang'a, L., 2015b. Understanding watershed dynamics and impacts of climate change and variability in the Pangani River Basin , Tanzania. Ecohydrol. Hydrobiol. 15, 26–38.

Larsen, S., Bruno, M.C., Vaughan, I.P., Zolezzi, G., 2019. Testing the River Continuum Concept with geostatistical stream-network models. Ecol. Complex. 39, 1–12.

Lessard, J.L., Hayes, D.B., 2003. Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. River Res. Appl. 19, 721–732.

Lewis, W.M., 2008. Physical and Chemical Features of Tropical Flowing Waters.In: D. Dudgeon, editor. Tropical Stream Ecology. Elsevier Inc., USA.

Li, F., Cai, Q., Liu, J., 2009. Temperature-Dependent Growth and Life Cycle of Nemoura sichuanensis (Plecoptera: Nemouridae) in a Chinese Mountain Stream. Hydrobiologia 94, 595–608.

Li, F., Chung, N., Bae, M., Kwon, Y., Park, Y., 2012. Relationships between stream macroinvertebrates and environmental variables at multiple spatial scales. Freshw. Biol. 57, 2107–2124.

Lintern, A., Webb, J.A., Ryu, D., Liu, S., Waters, D., Leahy, P., 2018. Key factors in fluencing differences in stream water quality across space. WIREs 5, 1–31.

Lumbreras, A., Marques, J.T., Belo, A.. ., Cristo, M., Fernandes, M., Galioto, D., Machado, M., Mira, A., Sá-Sousa, P., Silva, R., Sousa, L.., Pinto-Cruz, C., 2016. Assessing the conservation status of Mediterranean temporary ponds using biodiversity : a new tool for practitioners. Hydrobiologia 782, 187–199.

Malmqvist, B., Rundle, S.D., 2002. Threats to the Running Water Ecosystems of the World. Environ. Conserv. 29, 134–153.

Marques, M.M., Barbosa, F.A., Callisto, M., 1999. Distribution And Abundance Of Chironomidae (Diptera , Insecta) In An Impacted Watershed In South-East Brazil. Rev. Bras. Biol. 59, 553–561.

Masese, F.O., 2015. Dynamics in Organic Matter Processing , Ecosystem Metabolism and Trophic Sources for Consumers in the Mara River , Kenya.UNESCO-IHE Institute for Water Education.

Mcguire, K.J., Torgersen, C.E., Likens, G.E., Buso, D.C., Lowe, W.H., Bailey, S.W., 2014. Network analysis reveals multiscale controls on streamwater chemistry. Proc. Natl. Acad. Sci. U.S.A. 1–6.

Merritt, R.W., Cummins, K.W., Berg, M.B., 2008. An introduction to the Aquatic Insects of North America. Kendall / Hunt Publishing Company, Dubuque, Iowa.

Mouri, G., Takizawa, S., Oki, T., 2011. Spatial and temporal variation in nutrient parameters in stream water in a rural-urban catchment, Shikoku, Japan: Effects of land cover and human impact. J. Environ. Manage. 92, 1837–1848.

Msovu, U.E., Mulungu, D.M.M., Nobert, J.K., Mahoo, H., 2019. Land Use/Cover Change and their Impacts on Streamflow in Kikuletwa Catchment of Pangani River Basin, Tanzania. Tanzania J. Eng. Technol. 38, 171–191.

Munishi, L.K., Sawere, P.C., 2014. Climate change and decline in water resources in Kikuletwa Catchment, Pangani, Northern Tanzania. African J. Environ. Sci. Technol. 8, 58–65.

Mwamila, T.B., Kimwaga, R.J., Mtalo, F.W., 2008. Eco-hydrology of the Pangani River downstream of Nyumba ya Mungu reservoir , Tanzania. Phys. Chem. Earth 33, 695–700.

Naman, S.M., Rosenfeld, J.S., Richardson, J.S., 2016. Causes and consequences of invertebrate drift in running waters : from individuals to populations and trophic fluxes. Can. J. Fish. Aquat. Sci. 73, 1292–1305.

National Bureau of Statistics, 2013. The United Republic of Tanzania, 2012 Population and Housing Census, Population Distribution by Administrative Areas. Tanzania.

Nhiwatiwa, T., Brendonck, L., Dalu, T., 2017a. Understanding factors structuring zooplankton and macroinvertebrate assemblages in ephemeral pans. Limnologica 64, 1–26. h

Nhiwatiwa, T., Brendonck, L., Waterkeyn, A., Vanschoenwinkel, B., 2011. The importance of landscape and habitat properties in explaining instantaneous and long-term distributions of large branchiopods in subtropical temporary pans. Freshw. Biol. 56, 1992–2008.

Nhiwatiwa, T., Dalu, T., Brendonck, L., 2017b. Impact of irrigation based sugarcane cultivation on the Chiredzi and Runde Rivers quality, Zimbabwe. Sci. Total Environ. 587-588, 316–325.

Nhiwatiwa, T., Dalu, T., Sithole, T., 2017c. Assessment of river quality in a subtropical Austral river system : a combined approach using benthic diatoms and macroinvertebrates. Appl. Water Sci. 7, 4785–4792.

Oertli, B., Indermuehle, N., Angélibert, S., Hinden, H., Stoll, A., 2010. Macroinvertebrate assemblages in 25 high alpine ponds of the Swiss National Park (Cirque of Macun) and relation to environmental variables, in: Oertli, B., Céréghino, R., Biggs, J., Declerck, S., Hull, A. & Miracle, M. R. (eds.) Pond Conservation in Europe. Dordrecht: Springer Netherlands. pp. 29–41.

Özkan, N., Moubayed-Breil, J., Çamur-Elipek, B., 2010. Ecological Analysis of Chironomid Larvae (Diptera , Chironomidae) in Ergene River Basin (Turkish Thrace). Turkish J. Fish. Aquat. Sci. 10, 93–99.

PBWO/IUCN, 2007a. IUCN Water and Nature Initiative and Pangani Basin Water Board. River Health Assessment Final Report, Pangani River Basin Flow Assessment. Moshi Tanzania.

PBWO/IUCN, 2007b. Pangani River System: State of the Basin Report 2007. Moshi, Tanzania.

Peterson, E.E., Merton, A.A., Theobald, D.M., Urquhart, N.S., 2006. Patterns of Spatial Autocorrelation in Stream Water Chemistry. Environ. Monit. Assess. 121, 571–596. h

Peterson, E.E., Ver Hoef, J.M., 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks. Ecology 91, 644–651.

Peterson, E.E., Ver Hoef, J.M., 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks. Ecology 91, 644–651.

Poff, L.N., Allan, D.J., Bain, M.B., Karr, J.R., Prestegaard, K.L., Ritcher, B.D., Richard, S.E., Stromberg, J.C., 1997. The Natural Flow Regime A Paradigm for River Conservation and Restoration. Bioscience 47, 770–784.

Poole, G.C., 2002. Fluvial landscape ecology : addressing uniqueness within the river discontinuum. Freshw. Biol. 47, 641–660.

PWBO/IUCN, 2010. Climate change modelling for the Pangani Basin to support the IWRM planning process. Pangani River Basin Flow Assessment. Pangani Basin Water Board, Moshi and IUCN Eastern and Southern Africa Regional Programme.

Quinn, J.M., Cooper, A.B., Colley, R.J.D., Rutherford, J.C., Williamson, R.B., 1997. Land use effects on habitat , water quality , periphyton , and benthic invertebrates in Waikato , New Zealand , hill-country streams. New Zeal. J. Mar. Freshw. Res. 31, 579–597.

Richards, C., Haro, R.J., Johnson, L.B., Host, G.E., 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. Biol. 37, 219–230.

Richards, C., Host, G., 1994. Examining Land Use Influences on Stream Habitats and Macroinvertebrates: A Gis Approach. Am. Water Resour. Assoc. 30, 729–738.

Roiz, D., Ruiz, S., Soriguer, R., Figuerola, J., 2015. Landscape Effects on the Presence, Abundance and Diversity of Mosquitoes in Mediterranean Wetlands. PLoS One 10, 1–17.

Rosemond, A.D., Pringle, C.M., Ramirez, A., 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. Freshw. Biol. 39, 515–523.

Rosenberg, D.M.., Resh, V.H., 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. Ecology 75, 267–268.

Rostami, S., He, J., Hassan, Q.K., 2018. Riverine Water Quality Response to Precipitation and Its Change. Environments 5, 1–17.

Rouquette, J.R., Dallimer, M., Armsworth, P.R., Gaston, K.J., Maltby, L., Warren, P.H., 2013. Species turnover and geographic distance in an urban river network. Divers. Distrib. 19, 1429–1439.

Selemani, J.R., Zhang, J., Muzuka, A.N.N., Njau, K.N., Zhang, G., Mzuza, M.K., Maggid, A., 2017. Nutrients' distribution and their impact on Pangani River Basin's ecosystem – Tanzania. Environ. Technol. 702–716.

Shaghude, Y.W., 2006. Review of Water Resource Exploitation and Landuse Pressure in the Pangani River Basin. West. Indian Ocean J. Mar. Sci. 5, 195–207.

Sinha, A., Chatterjee, N., Ormerod, S.J., Adhikari, B.S., Krishnamurthy, R., 2019. River birds as potential indicators of local- and catchment-scale influences on Himalayan river ecosystems River birds as potential indicators of local- and catchment-scale influences on Himalayan river ecosystems. Ecosyst. People 15, 90–101.

Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation : Recent progress and future challenges. J. North Am. Benthol. Soc. 29, 344–358. https://doi.org/10.1899/08-171.1

Syvitski, J.P.M., Cohen, S., Kettner, A.J., Brakenridge, G.R., 2014. Geomorphology How important and different are tropical rivers ? - An overview. Geomorphology 227, 5–17.

Thiery, A., 1991. Multispecies coexistence of branchiopods (Anostraca, Notostraca & Spinicaudata) in temporary ponds of Chaouia plain (western Morocco): sympatry or syntopy between usually allopatric species. Hydrobiologia 212, 117–136.

Torres, M.V., Giri, F., Collins, P.A., 2018. Temporal and spatial patterns of freshwater decapods associated with aquatic vegetation from floodplain rivers. Hydrobiologia 823, 169–189.

Tudesque, L., Tisseuil, C., Lek, S., 2014. Scale-dependent effects of land cover on water physico-chemistry and diatom-based metrics in a major river system , the Adour-Garonne basin (South Western France). Sci. Total Environ. 466-467, 47–55.

URT, 2012. Guidelines for water resorces monitoring and pollution control. Ministry of Water. Dar es Salaam, Tanzania.

URT, 2002. The National Water Policy. Ministry of Water. Dar es Salaam, Tanzania.

Van den Broeck, M., 2016. Monitoring and conservation of Maediterranean temporary ponds. KU Leuven, Belgium.

Van den Broeck, M., Rhazi, L., Waterkeyn, A., Madihi, E.M., Grillas, P., Kneitel, J.M., Brendonck, L., 2019. Livestock disturbances in Mediterranean temporary ponds : A mesocosm experiment with sheep manure and simulated trampling. Freshw. Biol. 64, 856–869.

Van den Broeck, M., Waterkeyn, A., Rhazi, L., Brendonck, L., 2015a. Distribution, Coexistence, and Decline of Moroccan Large Branchiopods. J. Crustac. Biol. 35, 355–365.

Van den Broeck, M., Waterkeyn, A., Rhazi, L., Grillas, P., Brendonck, L., 2015b. Assessing the ecological integrity of endorheic wetlands , with focus on Mediterranean temporary ponds. Ecol. Indic. 54, 1–11.

Vannote, R.L., Minshall, G.W., Cummins, K., Sedell, J.R., 1980. The River Continuum Concept. Can J Fish Aquat Sci 37, 130–7.

Vannote, R.L., Minshall, W.G., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37, 130–137.

Vanschoenwinkel, B., Hulsmans, A., De Roeck, E., De Vries, C., Seaman, M., Brendonck, L., 2009. Community structure in temporary freshwater pools : disentangling the effects of habitat size and hydroregime. Freshw. Biol. 54, 1487–1500.

Ver Hoef, J.M., Peterson, E., Theobald, D., 2006. Spatial statistical models that use flow and stream distance. Environ.Ecol.Stat 13, 449–464.

Ver Hoef, J.M., Peterson, E.E., 2010. A Moving Average Approach for Spatial Statistical Models of Stream Networks. J. Am. Stat. Assoc. 105, 1–18.

Vörösmarty, C.J., Mcintyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Vo, C.J., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561.

Wantzen, K.M., Ramirez, A., Winemiller, K.O., 2006. New vistas in Neotropical stream ecology-Preface. J. North Am. Benthol. Soc. 25, 61–65.

Ward, J. V, Stanford, J.A., 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regul. riversResearch Manag. 11, 105–119.

Waterkeyn, A., Grillas, P., De Roeck, E.R.M., Boven, L., Brendonck, L., 2009. Assemblage structure and dynamics of large branchiopods in Mediterranean temporary wetlands : patterns and processes. Freshw. Biol. 54, 1256–1270.

Williams, D.D., 2006. The biology of temporary waters. Oxford Biology, pp. 268.

Wright, J.., Moss, D., Armitage, P.., Furse, M.., 1984. A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. Freshw. Biol. 14, 221–256.

WWF, 2006. Climate Change Impacts on East Africa: A Review of the Scientific Literature.

Summary

River ecosystems encompass river channels and its floodplains and form a diverse mosaic of habitats upon which countless species of animals and plants depend for survival. They provide a plethora of services for humans including a source of clean water for domestic and industrial uses, a source of food, a means of waste disposal, transportation, power production, and sites for the pursuit of leisure activities. Yet, they belong to the most threatened ecosystems on earth. Major threats to river ecosystems include habitat degradation, water pollution, flow modification, overexploitation, and invasion by exotic species. This is especially true for (sub) tropical developing countries where intensification of land-use for agriculture and poor disposal of untreated waste have markedly degraded rivers and associated floodplain ecosystems. Nevertheless, a proper understanding of ecosystem functioning and biological diversity is lacking. In this Ph.D., we contribute to bridging this knowledge gap. We investigate different factors that explain biodiversity and ecosystem quality in (afro) tropical river systems and associated temporary pool ecosystems in northeastern-Tanzania by using macroinvertebrates as biological indicators and collecting environmental and biological data at various spatial-temporal scales.

Firstly, we assessed how seasonality (i.e., wet and dry seasons) influences macroinvertebrate community structure and water quality conditions (Chapters 1 and 2). An extensive repeated-sampling survey was conducted to measure water quality, macroinvertebrates, and other presumed important environmental variables in the two sub-catchments of the Upper Pangani River Basin (UPRB). We found evidence that water quality conditions and macroinvertebrate assemblages differ between seasons and that these differences are associated with high flow velocity, and runoff carrying sediment and nutrient loads from the catchment area to the river systems during the rainy season. Moreover, our results revealed that chlorophyll-a, oxygen and phosphorous (dry season), nitrogen and turbidity (wet season), and substrate composition and agricultural land-use (both seasons) are important determinants for the variation in macroinvertebrates assemblages between sites. We also attempted to identify indicator taxa linked to specific water quality conditions and found that families Hydropsychidae (Trichoptera), Potamonautidae (Decapoda), Baetidae (Ephemeroptera), and Heptageniidae (Ephemeroptera) showed to be indicator taxa of good water quality conditions, while Hirudinea (Annelida) and Chironomidae (Diptera) appeared to be indicator taxa of poor water quality conditions (Chapter 1). Secondly, we focused on the impact of land-use at different spatial scales on river quality (Chapters 1 and 2). To quantify this we used three different spatial methods of land-use estimation; (i) land-use of the entire watershed area above the monitoring site, (ii) a circular buffer around a monitoring site, and (iii) a circular buffer immediately upstream of a monitoring site, with circular buffers varying from 100m to 2km. The land-use percentage compositions in the dry and wet seasons were quantified using Landsat-8 satellite images with a maximum mapping resolution of 30m. We found that physico-chemical water quality and macroinvertebrate assemblages responded differently to land-uses at different scales in both dry and wet seasons. Nevertheless, the relationships were not always straightforward and clearly scale-dependent,

suggesting that the spatial estimate used, and the spatial scale considered can strongly confound the conclusions (Chapter 2). Land-use of the entire watershed area upstream of the monitoring site better explained variation in physico-chemical water quality and macroinvertebrate indices whereas macroinvertebrate abundances showed strong links with more local land-use patterns within 100m and 2km radii. In Chapter 3, we added the main constraint that is not always included in studies of river systems i.e., connectivity and spatial autocorrelation among sites. For this, we use a spatially explicit analysis framework (spatial stream network (SSN) models) to test to what extent dendritic stream network structure affects spatial patterns of benthic macroinvertebrates and water chemistry at the catchment scale. We showed that spatial patterns and spatial autocorrelation exist in stream water chemistry and macroinvertebrate indices at both fine- and broad- spatial scale comprising both flow-connected and flow-unconnected spatial relationships. And that SSN models managed to make good predictions of water chemistry concentrations and macroinvertebrate indices at unsampled sites with estimates of uncertainty. The results highlight the value of SSN models and stress the need to specify spatial dependencies representing the dendritic network structure of river ecosystems. Finally, we assessed to what extent the seasonal connectivity of the river with temporary wetlands in the surrounding landscape is a crucial determinant of aquatic communities and environmental conditions in the floodplain wetlands. This was achieved by comparing environmental conditions and diversity and composition of macroinvertebrate communities from river connected pools with endorheic pools (Chapter 4). Macroinvertebrate communities from the two habitats were clearly differentiated and spatial taxon turnover was the main determinant of variation in community composition among pools. Hydrological connectivity facilitated the migration of fish to the river connected pools which structured the invertebrate community assemblages through selective predation, particularly of large prey such as large branchiopod crustaceans. Based on our dataset we identified indicator taxa for the different habitat types and found no specific fauna unique to river connected pools.

Overall, our results suggest monitoring of river systems in wet and dry seasons given the fact that different selective filters limit invertebrate assemblages in both seasons. We recommend the creation of intact riparian buffer zones of at least 60 m from each side of the riverbank to help alleviate some of the observed negative effects of the land-use activities on the river systems. In addition, conservation and management schemes of temporary pools should focus on both river connected and endorheic pools to support high regional diversity. More importantly, SSN models should be used to support river basin management in the region in a rapid and cost-effective way.

Samenvatting

Rivierecosystemen omvatten de riviergeul en zijn overstromingsvlaktes, en vormen een diverse mozaïek van leefgebieden die voor talrijke dier- en plantensoorten levensnoodzakelijk zijn. Ze voorzien een veelheid aan diensten voor mensen, zoals schoon water voor huishoudelijk en industriël gebruik, een bron voor landbouwproductie, een manier van afvalverwijdering, transport, energieproductie, en recreatie. Toch behoren ze tot de meest bedreigde ecosystemen op aarde. De grootste bedreigingen van rivierecosystemen zijn habitatverlies, watervervuiling, stroomwijzigingen, overexploitatie en invasie door exotische soorten. Dit geldt voornamelijk voor (sub)tropische ontwikkelingslanden, waar de intensivering van landgebruik door landbouw, en het slecht afvoeren van onbehandeld afval, een duidelijk negatieve invloed op de rivieren en hun bijhorende overstromingsvlaktes hebben gehad. Desalniettemin ontbreekt inzicht in hoe het rivierecosysteem werkt, en de biodiversiteit die het herbergt. Met dit doctoraatsonderzoek willen we bijdragen tot het opvullen van deze lacune. We onderzoeken verschillende factoren die biodiversiteit en ecosysteemkwaliteit verklaren in (afro) tropische riviersystemen en geassocieerde tijdelijke poel ecosystemen in noordoost Tanzania, gebruikmakend van macro-invertebraten als biologische indicator en door het verzamelen van omgevings- en biologische data op verschillende ruimtelijke- en tijdsschalen.

Eerst schatten we in hoe seizoenaliteit (zijnde het nat en droog seizoen) de structuur van de macro-invertebraten gemeenschap en waterkwaliteitscondities beïnvloed (Hoofdstuk 1 en 2). Een uitgebreid herhaaldelijk staalname onderzoek werd uitgevoerd om waterkwaliteit, macro-invertebraten en andere, vermoedelijk belangrijke omgevingsvariabelen, te meten in twee deelstroomgebieden van het Upper Pangani River Basin (UPRB). We vonden bewijs dat waterkwaliteitscondities en de samenstelling van macro-invertebraat gemeenschappen verschillen tussen seizoenen, en dat deze verschillen geassocieerd zijn met een hogere stroomsnelheid en afvoer van sediment en nutriënten van het stroomgebied naar de riviersystemen gedurende het regenseizoen. Bovendien onthulden onze resultaten dat chlorofyl-A, zuurstof en fosfor (droog seizoen), stikstof en troebelheid (nat seizoen), de samenstelling van de ondergrond en landbouwgebruik (beide seizoenen), belangrijke factoren zijn die de variatie in samenstelling van macro-invertebraat gemeenschappen verklaren tussen sites. We probeerden ook om indicator taxa te identificeren die gelinkt kunnen worden aan specifieke water condities en vonden dat de famillies Hydropsychidae (Trichoptera), Potamonautidae (Decapoda), Baetidae (Ephemenopthera), en Heptageniidae (Ephemenopthera) een indicator zijn van goede waterkwaliteit, terwijl Hirudinea, (Annelida) en Chironomidae (Diptera) een indicator bleken te zijn van slechte waterkwaliteit (Hoofdstuk 1 en 2). Ten tweede focusten we ons op de inpakt van landgebruik op verschillende ruimtelijke schalen op de kwaliteit van de rivier (Hoofdstuk 2). Om dit te kwantificeren gebruikten we drie verschillende ruimtelijke methodes om het landgebruik in te schatten; (i) landgebruik van het volledige waterscheidingsgebied boven de monitoring site, (ii) een cirkelvormige buffer rond de monitoring site en (iii) een cirkelvormige buffer onmiddellijk stroomopwaarts van de monitoring site, de cirkelvormige buffers met een radius variërend van 100 m tot 2 km. De samenstelling van de landgebruikspercentages in het droge en natte seizoen werden gekwantificeerd gebruikmakende van Landsat-8 satelliet afbeeldingen met een maximale resolutie op kaart van 30 m. We vonden dat de fysicochemische waterkwaliteit en de samenstelling van macro-invertebraat gemeenschappen anders reageerden op landgebruik op verschillende schaal in zowel het droge als natte seizoen. Desalniettemin waren de relaties niet altijd rechtlijnig en duidelijk schaal afhankelijk, dit doet vermoeden dat de ruimtelijke schatting die werd gebruikt, en de ruimtelijke schaal die beschouwd werd, de conclusie sterk kunnen beïnvloeden (Hoofdstuk 2). Landgebruik van het volledige waterscheidingsgebied stroomopwaarts van de monitoring site kon variatie in fysicochemische waterkwaliteit en macro- invertebraat indicatoren beter verklaren, terwijl de hoeveelheid macro-invertebraten een sterke link vertoonden met meer lokale landgebruikspatronen binnen de 100 m en 2 km radius. In hoofdstuk 3 voegden we de factoren toe die meestal niet aanwezig zijn in studies naar riviersystemen, zijnde connectiviteit en ruimtelijke autocorrelatie tussen sites. Hiervoor gebruikten we een ruimtelijke expliciet analytisch kader (spatial stream network SNN model) om te testen tot in hoeverre de structuur van een vertakt stroomnetwerk de ruimtelijke patronen van benthische macro-invertebraten en chemische kenmerken van het water beïnvloed op het niveau van het stroomgebied. We toonden aan dat ruimtelijke patronen en ruimtelijke autocorrelatie bestaat in de chemische kenmerken van stromend water en macro-invertebraat indicatoren in zowel fijn- als breedruimtelijke schaal, bestaande uit ruimtelijke relaties die zowel stroomgebonden als niet- stroomgebonden zijn. Daarnaast toonden we ook aan dat SNN modellen goede voorspellingen kunnen maken van de concentraties van chemische kenmerken van water en macro-invertebraat-indicatoren op sites waar geen stalen werden genomen met een marge van onzekerheid. De resultaten duiden op het belang van SNN modellen en verhogen de druk op het noodzakelijk weergeven van de ruimtelijke afhankelijkheid van de het vertakte netwerkt van de structuur van de rivierecosystemen. Tot slot beoordeelden we in hoeverre de seizoenale connectiviteit van de rivier met tijdelijk drasland in het omgevende landschap een cruciale verklarende factor is voor watergemeenschappen en omgevingscondities in het drasland van de stroomgebieden. Dit werd bereikt door de omgevingscondities, diversiteit en samenstelling van de macro-invertebraat gemeenschappen van poelen die in verbinding staan met de rivier te vergelijken met poelen die niet in verbinding staan met een ander waterlichaam (Hoofdstuk 4). Macro-invertebraat gemeenschappen van deze twee soorten leefgebieden verschilden duidelijk en ruimtelijke taxon verandering was de belangrijkste verklarende factor van variatie in gemeenschapssamenstelling tussen poelen. Hydrologische connectiviteit vergemakkelijkt migratie van vis naar de poelen en structureert de samenstelling van de macro-invertebraten gemeenschap door selectieve predatie, voornamelijk van grotere prooien zoals grote kieuwpootkreeftjes. Gebaseerd op onze dataset probeerden we indicator taxa te identificeren voor de verschillende types leefgebied, en vonden geen specifieke fauna uniek voor poelen die in verbinding staan met een rivier.

In het algemeen suggereren onze resultaten dat monitoring van riviersystemen zowel in het droog als nat seizoen dient te gebeuren, vermits verschillende selectieve filters de samenstelling van de gemeenschap macro-invertebraten limiteren in beide seizoenen. We raden de aanleg van intacte oeverzones van minstens 60 meter breed langs beide zijden van de rivierbedding aan om sommige van de negatieve effecten van het landgebruik op de riviersystemen te verminderen. Daarnaast dienen behouds- en beheerschema's van tijdelijke poelen zich te focussen op zowel rivier geconnecteerde als afgesloten poelen om een hoge regionale diversiteit te ondersteunen. Nog belangrijker, SNN modellen zouden gebruikt moeten worden om het beheer van rivierbekkens in de regio te ondersteunen op een snelle en kosteneffectieve manier.

List of Scientific Publications

i. **Mwaijengo, G.N.**, Msigwa, A., Nicholas, K., Brendonck, L., Vanschoenwinkel, B., 2020. Where does land use matter most? Contrasting land use effects on river quality at different spatial scales. Science of the Total Environment. 715, 1–14. https://doi.org/10.1016/j.scitotenv.2019.134825

ii. **Mwaijengo, G.N.,** Vanschoenwinkel, B., Dube, T., Njau, K.N., Brendonck, L., 2020. Seasonal variation in benthic macroinvertebrate assemblages and water quality in an Afrotropical river catchment, northeastern Tanzania. Limnologica. 82, 1-12. https://doi.org/10.1016/j.limno.2020.125780

iii. Dube, T., de Necker, L., Wepener, V., Smit, N.J., Pinceel, T., **Mwaijengo, G.N.,** Brendonck, L., 2020. A comparison of aquatic macroinvertebrate and large branchiopod community composition between temporary pans of a conservation area and surrounding communal area in South Africa. African Zoology. 55, 1–11. https://doi.org/10.1080/15627020.2020.1724827