Modelling flow and water temperature in the Luvuvhu catchment and their impact on macroinvertebrate assemblages

Ramulifho Pfananani Anania

Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Zoology

School of Mathematical and Natural Sciences
University of Venda
Thohoyandou, Limpopo
South Africa

12 December 2019

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Dedication

This thesis is dedicated to my Father,

(Ramulifho Phineas Pandiani,

Who lost the battle to illness on the 13th November 2018.

He is always in my memory)

And

To all rivers of the Luvuvhu catchment,

For their unceasing provision of ecological services, despite all the pain of mismanagement, pollution, and unbearable abstraction we subject them to.

Preface

The work described in this thesis was carried out in the School of Mathematics and Natural Sciences, in the department of Zoology, under the SARChI chair on Biodiversity Value and Change in the Vhembe Biosphere Reserve, University of Venda, Thohoyandou, from January 2016 to December 2019, under the supervision of Professor Stefan Foord and Doctor Nick Rivers-Moore.

Abstract

Stream flow and water temperature regimes are master variables driving river ecosystems, which determine the spatial and temporal dynamics of plant, benthic and other taxonomic groups in streams. Stream flow and water temperature trends are changing drastically worldwide with far-reaching effects on aquatic organisms. These changes are predicted to be disproportionately higher in southern Africa compared to most other regions of the world, due to declining and unreliable rainfall, increasing human population and changing land and water uses. In this study, these issues were investigated in the Luvuvhu River catchment (LRC), a strategic water source area in an arid region of southern Africa. Stream flow in the LRC is currently subjected to major forms of flow alteration, including large dams and abstraction. Studies on long-term changes in stream flow and water temperature regime are limited in this catchment. Given the fact that these rivers are home to many flow and temperature sensitive aquatic organisms such as mayflies and blackflies, the current situation in the LRC raises important concerns around the hydraulic and thermal stress of these biota. Making things worse, very few studies have assessed the constraints towards the development of conservation and management programs for rivers and their related ecosystem services in the LRC.

Assessment of long-term changes in stream flow patterns, correlation between sub-daily and daily flow metrics, the influence of stream flow, water temperature and other environmental variables on both mayfly and blackfly assemblage structure and also the identification the indicator species along important environmental gradients were the main objectives of this study. This study also reviewed institutional challenges affecting the sustainable management of stream flow and river management frameworks to provide environmental flows. Flow gauging stations were selected across the catchment based on the availability of long-term (> 20 years) stream flow data, while mayfly and blackfly organisms were collected from twenty-three sites for not less than twelve months together with the measurements of flow, water temperature and other environmental variables.

All stream flow trend analyses pointed to declining stream flow volumes that are most pronounced during the wet seasons. This declining stream flow volumes are occurring in both tributaries and main river channels. Stream flow monitoring is poor in the LRC with flow at most of the stations not natural, where only one gauging station had natural flow records. However, most of the natural sub-daily flow metrics (for example, daily minimum, daily maximum, daily delta, standard deviation, maximum hourly ramp rate, daily path length, and daily standardized delta) were related to daily flow metrics. Water temperature is slowly but significantly rising, while climatic data showed that in rainfall and air temperature in the catchment had no significant change over the last 35 years. The absence of catchment specific management institutions and strategies to address issues such as water allocation and conservation is one of the major problem in the LRC, and these has implication for aquatic biota as the habitat continues to deteriorate. Water temperature is the major driver of mayfly structure and richness. Stream flow explained some considerable amount of variation, while a large proportion of variation in blackfly community structure remained unexplained. Majority of mayflies are cold water species and are threaten by changing water temperature (> 19 °C), while blackfly species respond positively to increasing flow. The development and implementation of catchment-wide flow management strategies and abstraction thresholds would make a major contribution in minimizing the declining stream flow volumes in rivers of the LRC. To save aquatic biota in the LRC, a key focus for impounded rivers should be the provision of environmental flows for restoration of habitat for aquatic species, while for non-regulated rivers, the most effective option is to conserve and maintain their free-flowing condition. Stream flow monitoring and reporting should be prioritized to give regular accounts of the health of our rivers.

Manweledzo a ngudo

Mutakalo wa mupo, miri, na zwikhokhonono zwa madini zwi laulwa (langwa) na u tutuwedzwa nga mufhiso wa lutsinga lwa madi milamboni. Nga vhanga la mupo une wa khou shanduka nga ndila ya vhuhali, kufhisele kwa madi milamboni ku khou Shanduka. Hezwi zwina masia ndoitwa asi a vhudi kha kutshilele kwa zwikhokhonono milamboni. Tshanduko hedzi dzi ntha lwo kalulaho tshipembe ha Afrika, ri tshi vhambedza na vhunwe vhupo kha lifhasi. Kha ino thoduluso, ro guda milambo ya govha lothe la Luvuvhu, hune havha fhethu ho khetheaho ngeha dalesa madi.

Nyelelo ya madi milamboni ya govha la Luvuvhu yo no thithiswa nga madamu na migero i no khou dzhia madi nga ndila ya usa londa, vhadzulapo na vhashumisi vha madi. Ngudo dzingaho hedzi dza tshanduko ya kutshilele nau anda ha zwikhokhonono, na zwinwe zwitshilaho madini adzi athu u dala kha heyi milambo na vhupo hashu. Mbudziso ine heyi thoduluso ya khou linga uyi tandulula ndi ya uri, nga fhasi ha mutsiko mungafha wa tshanduko ya mupo, izwi zwikhokhonono zwa madini zwi khou kona hani u tshila. Asi ngudo nnzhi dzine dzo no sedza fhungo la u savha hone ha mbetshelwa na thandela dzau tsireledza milambo na mishumo yayo kha govha ili la Luvuvhu.

Thoduluso dza tshanduko kha nyelelo ya madi kha tshifhinga tshilapfu, thuthuwedzo ya lutsinga lwa madi milamboni, mufhiso wao na zwinwe zwiga zwa mupo zwono tutuwedza u phadalala na mifuda ya zwikhokhonono, nau nanga zwikhokhonono zwa tsumba tshanduko ya mupo zwovha zwone zwi pikwa zwa ngudo iyi. Zwi tshiya phanda, rodovha ra todulusa khaedu kha zwiimisa zwi langaho milambo na nyelelo ya madi. Zwititshi zwau sedza madi milamboni ho nangwa zwezwa wanala zwina vhutanzi ha nyelelo ya madi ifhiraho minwaha ya mahumi mavhili, ngeno zwikhokhonono zwo sengedza ubva kha vhupo vhu linganaho mahumi mavhili na raru lwa tshifhinga tshi fhiraho nwaha kha eneyi miyambo.

Thoduluso dzothe dzo sumba uri nyelelo ya madi ikhou fhungudzea, zwihuluhulu nga tshilimo. Hezwi zwi kwama milambo yothe, mituku na mihulwane. U sedza nyelelo ya madi zwo tutshelwa kha govha lothe la Luvuvhu, ngeno madi a satsha elela nga ndila ya mupo, hune hoto wanala fhedzi

huthihi hu songo thithiswaho. Nyelelo ya madi fhethu afho musi yo sedza nga tshifhinga tsha fhasi ha iri, ifana na nyelelo ya madi yo kalwa nga tshifhinga tshi linganaho duvha lithihi. Ro wana uri mvula na mufhiso wa muya azwongo shanduka lwa minwaha ya mahumi mararu na mitanu yo fhiraho. U savha hone ha tshiimiswa tshoto sedzanaho na milambo ya govha leli, zwikhou nanisa thaidzo ya u xa na usa tsireledzea ha milambo. Hezwi zwi khou vha na masia ndoitwa o vhifhaho kha zwikhokhonono, ngeno milambo ikhou thothela. Ro wana uri mufhiso wa madi ndi wone ulangaho zwikhokhonono zwila zwononga zwisusu zwa madini ngeno nyelelo iyone ine ya tutuwedza u phadalala ha zwikhokhonono zwila zwononga zwivhungu madini. Vhunzhi ha zwokhokonono zwila zwononga zwisusu azwi andani na mufhiso na hone zwina khaedu yau nana ha mufhiso madini. Zwila zwononga zwivhungu zwi anda nga vhunzhi na nga mifuda musi nyelelo ya madi itshi engedzea. U sikwa nau tevhedzwa ha mbetshelwa yau langa nyelelo ya madi na ndila ine vhashumisi vha madi vhaka ngayo madi zwido fhungudza u xa ha madi milamboni. U tshidza zwikhokhonono zwa madini kha govha la Luvuvhu, milambo ine yavha na madamu ifanela u fhirisa madi a tse na mulambo kha tshikalo tshifhanaho na tsha mupo wone une. Ngeno milambo isina madumu ifanela u tsireledzwa uri i bvele phanda nau elela isa khakhiswi. U thogolela na tsivhudza ngaha milambo zwi fanela u dzhilelwa ntha uri mutakalo wa milambo yashu I divheye.

Acknowledgement

I thank God Almighty for his grace and for giving me strength and good health during the course of this study.

"Thou art worthy, O Lord, to receive glory and honour and power - Rev 4:11"

I am happy to also thank the following people and institutions for their contributions, who have made the start and completion of this thesis possible:

Professor Stefan Foord, Department of Zoology and Centre for Invasion Biology, University of Venda, for his amazing supervision and amazing knowledge. All his contributions, skills in R and thoroughly critiquing of the write up significantly benefited this study.

Dr. Nick Rivers-Moore, Centre for Water Resources Research, University of KwaZulu-Natal for his supervision and advice throughout the research process.

Ms Hermien Roux, Department of Zoology, University of Venda for her in-depth knowledge on rivers and guidance during all my field excursions and surveys.

Professor Peter Taylor, University of Venda, South African Research Chair in Biodiversity and Change Initiative (SARChI) of the National Research Foundation (NRF) for funding (F417) and support towards my research and conference.

Dr. Helen Dallas, Freshwater Research Centre, for her collaboration and support through the Water Research Commission (WRC project K5/2537) grant.

Albany Museum, Makhanda (Grahamstown), South Africa, I am grateful to Dr. Helen Barber James, Dr. Ferdy de Moor and Dr. Terence Bellingan for confirming and teaching me how to identify the larvae of Ephemeroptera and Simuliidae.

Research and Innovation Directorate, University of Venda, for providing funds towards (cost center number S778) running cost of this project.

Fananani Mbulaheni, Murunwa Nelufule, Lorraine Ramotjiki, Ratshibvumo Tshikambu, Ronewa Mulaudzi, Phindulo Thenga and many others, all from University of Venda, are thanked for fieldwork assistance, moral support and friendship throughout the research process.

Miss Pfariso Demana, for her unwavering support, love and patience during the course of this study.

Ramulifho Aluwani Elijah, for editing and improving the Tshivenda abstract of this thesis

My family (mom, siblings and niece), dad could not make it to see the completion of this study, but you have been my prime source of my motivation. Without your care, love, and prayers, this work would not have been possible.

A number of people have contributed in various ways towards the completion of this study. I am grateful to those who have offered assistance in any form. I thank you all.

Declaration – Plagiarism

I, Ramulifho Pfananani Anania, declare the work presented in this thesis is my own original work, and has not been presented in part or wholly for the award of a diploma or degree in any university. This thesis does not contain other person's writing unless specifically acknowledged and referenced accordingly.

Signature (student): .... Date: **11 December 2019**

Signature (supervisor): .... Date: **11 December 2019**

Signature (co-supervisor): A.J. Rivers-Moore Date: **11 December 2019**

Declaration – Publication

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part of and/or include research presented in this thesis (including publications submitted and published, giving details of the contributions of each author to the research and writing of each publication):

Publication 1 – Chapter 5 of this thesis

Ramulifho, PA, Ndou, E, Thifhulufhelwi, R, Dalu, T. 2019. Challenges to Implementing an Environmental Flow Regime in the Luvuvhu River Catchment, South Africa. Int. J. Environ. Res. Public Health 2019, 16, 3694; doi: 10.3390/ijerph16193694.

Ramulifho PA conceptualized idea. Ramulifho PA collected the data, analyzed and wrote the manuscript with the help of Dalu T. Ramulifho PA, Dalu T, Thifhulufhelwi R and Ndou E edited and gave scientific comments and suggestions and contributed to packaging the idea.

Publication 2 – Chapter 2 of this thesis

Ramulifho PA, Foord SH, Rivers-Moore NA, Roux H. 2019. Characterization of sub-daily flow and long-term stream flow changes using daily flow data in a rapidly developing arid region of southern Africa. *Submitted to Journal of Hydrology*.

Data collection, modelling and analysis of this publication was conducted by Ramulifho PA, with technical advice from Foord SH and Rivers-Moore NA. The publication was written in its entirety by Ramulifho PA. Figures, tables and graphs were produced by Foord SH and Ramulifho PA, unless otherwise referenced in the text of the paper. Editing and advice regarding interpretation was provided by Foord SH and Rivers-Moore NA.

Publication 3 – Chapter 3 of this thesis

Ramulifho PA, Foord SH, Rivers-Moore NA. 2019. The role of hydro-environmental factors in Mayfly (Ephemeroptera, Insecta) community structure: identifying threshold responses. *Submitted to Ecology and Evolution.*

Data collection and write-up of this publication were conducted by Ramulifho PA, with technical advice from Foord SH and Rivers-Moore NA. Modelling and analyses together with production of figures, tables and graphs were conducted by Foord SH and Ramulifho PA. Editing and advice regarding interpretation was provided by Foord SH and Rivers-Moore NA.

Publication 4 – Chapter 4 of this thesis

Ramulifho PA, Foord SH, Rivers-Moore NA. 2019. Blackfly assemblage distribution in streams of varying environmental gradients in the Luvuvhu catchment, South Africa. *In preparation and will be submitted to a scientific journal "African Journal of Aquatic Science".*

Data collection and write-up of this publication were conducted by Ramulifho PA, with technical advice from Rivers-Moore NA and Foord SH. Modelling and analyses together with production of figures, tables and graphs were conducted by Ramulifho PA and Foord SH. Editing and advice regarding interpretation was provided by Rivers-Moore NA and Foord SH.

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Chapter 1: General Introduction

1.1. Background

River scientists are challenged by the question of how much water a river needs to maintain its natural health and to sustain the integrity of aquatic and riparian ecosystems (Ramulifho et al 2019: Poff et al., 2010). Substantial evidence in literature prove beyond any reasonable doubt that a river's flow and water temperature regimes are important in sustaining biodiversity and ecological integrity (Bunn & Arthington, 2002; Caissie, 2006; Poff and Zimmerman 2010; Dallas and Rivers-Moore, 2014). Water temperature influences survivorship, growth, metabolism, fecundity, abundance and the distribution of aquatic organisms (Caissie, 2006), while stream flow regulates the distribution, abundance and diversity of aquatic organisms in streams and rivers (Poff and Zimmerman, 2010).

Studies on stream flow and water temperature trends worldwide have shown varying results, with a large number of studies pointing to profound changes (Milly et al., 2005, Kaushal et al., 2010; Kusangaya et al., 2013, Orr et al., 2015). Regions of the United States have recorded both increasing and decreasing streamflow (Medley et al., 2011), while no significant change in annual mean flow was found in southeastern Canada (Yue and Wang. 2002). No evidence of increasing annual average streamflow discharges in the Rhine River, while the annual average and seasonal discharges have hardly changed over the last century in central Europe (Wang et al., 2005). Less runoff occurred in southern Europe, southernmost South America, southern Australia and western mid-latitude North America (Milly et al., 2005), while the observed streamflow increases in the La Plate basin of southern South America, Southern through central North America, the south-eastern quadrant of Africa, and northern Australia (Zhang et al., 2011). There is a limited number of studies on long-term changes of streamflow in southern Africa (Odiyo et al., 2015), but the general conclusion is that streamflow is declining (Kusangaya et al., 2013). An assessment of 502 river flow gauging stations in nine countries of the southern African region found evidence of declining stream flow in parts of Zambia, Angola, Mozambique and the highveld in South Africa (Odiyo et al, 2016).

Though long-term trends in river water temperature are not well reported with the same spatial or temporal intensity as stream flow, studies from Europe and the United States suggest that the majority of large rivers are warming lately over the past two decides (Orr et al., 2015). The investigation of North America rivers shows a significant warming with a most rapid increase of 0.077˚C per year (Kaushal et al., 2010). Generalizations for overall trends in water temperature is problematic because the lack of data (Rivers-Moore et al., 2005), with most thermal data for southern Hemisphere rivers derived from ecological and hydrobiological studies (Dallas, 2008). However, long-term water temperature studies in many South African rivers show that water temperature is already widely compromised (Dallas and Rivers-Moore, 2014). The general conclusion drawn from remote sensing derived and observed air temperature records in southern Africa rivers is that minimum temperature is rising faster than maximum temperatures (Kruger and Shongwe, 2004; Kusangaya et al., 2013).

Stream flow is largely driven by hydrological and climatic factors, including overland flow and precipitation. The greatest of modifiers of hydrological drivers include anthropogenic flow manipulation in streams and rivers through impoundment, followed by water diversion and abstraction (Poff and Zimmerman, 2010). This has a direct influence on the thermal regime and natural habitat for aquatic organisms in rivers (Olden and Naiman, 2010). Global climate change drivers alter stream flow patterns (magnitude, duration and timing), increasing the frequency and intensity of extreme events (droughts and floods), and changing groundwater recharge rates (Dallas and Rivers-Moore, 2014). Drivers of water temperature can be grouped into hydrological, climatic and structural factors (Ramulifho et al., 2018). Hydrological drivers are natural water temperature regime modifiers and largely include human interventions such as water abstraction, impoundment, wastewater discharges, channel management and river flow regulation (Dallas, 2008; Orr et al., 2015). Climatic drivers include local climate gradients (precipitation, air temperature and evaporative demand), while valley slope, elevation, aspect, hill shading, channel incision and morphology, surface–groundwater interactions, catchment and riparian vegetation cover are some of the structural drivers (Poole and Berman, 2001; Caissie, 2006).

1.2. Relationship between stream flow and water temperature

Stream flow regime plays a central role in determining water temperature patterns. Water temperature in rivers is inversely related to discharge (Dallas, 2008), while in naturally flowing rivers, maximum temperatures generally increase downstream (Vannote et al., 1980; Palmer and O'Keeffe, 1989). Stream flow volume, as a function of river hydraulics (e.g. inflows and outflows), mainly influences the heating capacity and cooling of streams through mixing of water from different sources including streambed heat exchanges (Caissie, 2006). A reduction of stream flow, resulting from natural causes, water withdrawal or water diversion, has been shown to increase daily water temperatures, including daily maxima due to the lower corresponding depth of flow (Dallas, 2008). The extent to which flow from upstream impoundment modifies downstream water temperature depends on operational variables (release depth, discharge pattern) and the position of the impoundment in a river (Palmer and O’Keeffe, 1989). Both stream flow and water temperature regime can be decomposed into metrics describing the magnitude, timing, duration and frequency of flow and thermal events respectively (Olden and Naiman, 2010; Rivers-Moore et al., 2013).

Stream flow volume and patterns in rivers are the most manageable abiotic parameters (setting targets for flow rates), while indirect management of water temperatures is possible by targeting those drivers and buffers of thermal regimes that can be directly managed (Rivers-Moore and Jewitt, 2007). However, despite broad recognition of the importance of flow and thermal regimes for river systems, there are relatively few studies that have explicitly linked dam-induced changes in both flow and thermal factors to ecological structure and function (Arthington et al., 2006).

1.3. The influence of stream flow on aquatic macroinvertebrate

Stream flow regime drives aquatic organisms in several ways in space and time (Poff et al., 2010), with flow alteration often claimed to be the most serious and continuing threat to sustainability of biological organisms in rivers (Bunn & Arthington, 2002). Stream flow regulates the distribution, abundance and diversity of aquatic organisms in streams and rivers (Poff and Zimmerman, 2010), while also facilitating the movement of migratory aquatic organisms between accessible habitats (Bunn & Arthington, 2002). For example, the serious outbreaks of *Simuliium chutteri* in 2000, 2001 and 2011 were attributed to elevated levels of stream flow along the Orange River in South Africa (De Beer and Kappmeier Green, 2012; Rivers-Moore and Hill, 2018). Another example includes mayfly species such as *Centroptilum luteolum*, *Ephemera danica* and *Caenis horaria* which only inhabit slow-flowing or standing water bodies (Vilenica et al., 2017). A study by Yanai et al. (2018) also found that the distribution of *Baetis pacis* is only limited to small and medium-sized streams with moderate flow. This shows that stream flow changes as a result of anthropogenic activities and global climate change can cause alteration of community composition, decline of sensitive and endemic organisms, while promoting the invasions by exotic species (Bunn and Arthington, 2002; Poff and Zimmerman, 2010).

1.4. The influence of water temperature on aquatic macroinvertebrates

The thermal regime of rivers plays an important role in the overall health of aquatic organisms (Caissie, 2006), and is recognised as one of the most influential abiotic drivers of aquatic organisms' behaviour (Dallas and Rivers-Moore, 2014). Aquatic organisms' growth rate, metabolism, feeding rate, fecundity, emergence, behavior, survival and reproduction are all influenced by water temperature (Caissie, 2006; Haidekker and Hering 2008 Dallas and Rivers-Moore, 2012; Dallas and Ketley, 2011). Water temperature also governs the evolution, distribution and diversity of some of the species in rivers (Dallas, 2008; Dallas and Rivers-Moore, 2012; Svitok, 2006; Bauernfeind and Moog, 2000; Klonowska-olejnik and Skalski, 2014). In fact, aquatic organisms have specific temperature preferences, which can ultimately determine their distribution and development within streams (Caissie, 2006). This is a global phenomenon, as shown in a large number of modelling studies undertaken in many different environments, with several studies using global-scale models to estimate changes in regime across the global domain (Barber-James et al. 2008; Arnell and Gosling, 2013). For example, an observational study from streams in the of west of Europe shows that the distribution of a cold stenothermic mayfly species, *Baetis alpinus*, is limited to streams with temperature ranges between 5 and 13°C and this species optimal development takes place between 8 and 11°C (Haidekker, 2004). Most eggs of *Baetis rhodani* hatch in less than 10 days if temperatures exceed 10 °C, although in certain species extended hatching has been demonstrated in the laboratory and the field (Sartori and Brittain, 2015). Two eurytopic and eurythermic species, *Centroptilum luteolum* and *Serratella ignita* are found most commonly in habitats with moderate (<18 °C) and warmer water (≥18 °C) (Vilenica et al., 2017). A laboratory study by Dallas and Rivers-Moore (2018) showed that the chronic thermal stress threshold for *Lestagella penicillata* ranges from 19.2 °C in August to 20.7 °C in December. Changes in natural water temperature have important implications for biotic responses, and it is becoming clear that this variable is therefore worthy of study and understanding (Caissie, 2006).

1.5. Mayflies and blackflies as biological indicators of habitat change

Mayflies have been used extensively as biological indicators of environmental degradation in rivers (Kubendran et al., 2017). A number of studies have demonstrated that mayfly are effective indicators of stream flow and water temperature (Bauernfeind & Moog, 2000; Klonowska-olejnik and Skalski 2014; Kubendran et al., 2017). The mayfly group is widely used as water quality indicators by virtue of their widespread occurrence (Sartori and Brittain, 2015). Mayflies are distributed worldwide with over 3000 species, in more than 400 genera and 42 families (Barber-James et al. 2008), ubiquitous in every kind of freshwater ecosystem (Buss and Salles, 2007; Alhejoj et al., 2014), representing the largest purely aquatic invertebrate order in streams and rivers (Dijkstra et al., 2014). Mayflies are highly sensitive to substrate type, water velocity, depth, turbulence, temperature and other hydraulic parameters (Buss and Salles, 2007; Gustafson 2008; Vilenica et al. 2018), and have localized movement (Kubendran et al., 2017) which are all influenced by a river's thermal and flow signature (Rivers-Moore et al., 2013). The use of mayfly as indicators of a river's thermal and flow signature is considerably less expensive than the physio-chemical and desktop methods because it does not involve the use of expensive tools and mayflies are easy to collect (Buss and Salles, 2007). Moreover, it is an efficient technique, as it considers the ecological status of the system (Bauernfeind & Moog, 2000).

Blackfly larvae are found in most river systems worldwide (Zhang et al. 1998), and are frequently abundant in fast flowing water ecosystems (Kazanci, 2006). There are currently 2,175 extant species in the family with 1,820 recognised globally as belonging to the genus *Simulium* (de Moor, 2017). They inhabit most types of running waters (Feld et al., 2002; Figueiró et al., 2012). The composition of blackfly communities is closely related to various environmental variables, largely so to hydro-morphological conditions of running waters (Feld et al., 2002; Kazancı 2006). Larvae of different blackfly species prefer stones, submerged vegetation or any other firm substratum in moderate to swift-flowing waters and have limited locomotive powers (de Moor, 2017). Because of this preference for specific stream flow and water temperature conditions, blackfly larvae are good indicators of environmental degradation and restoration of streams and rivers (Feld *et al.* 2002, Zhang *et al.* 1998). Blackfly larvae have been widely used as biological indicators to assess the impact of anthropogenic activities in rivers (Ambelu et al., 2014).

1.6. Description of the study area

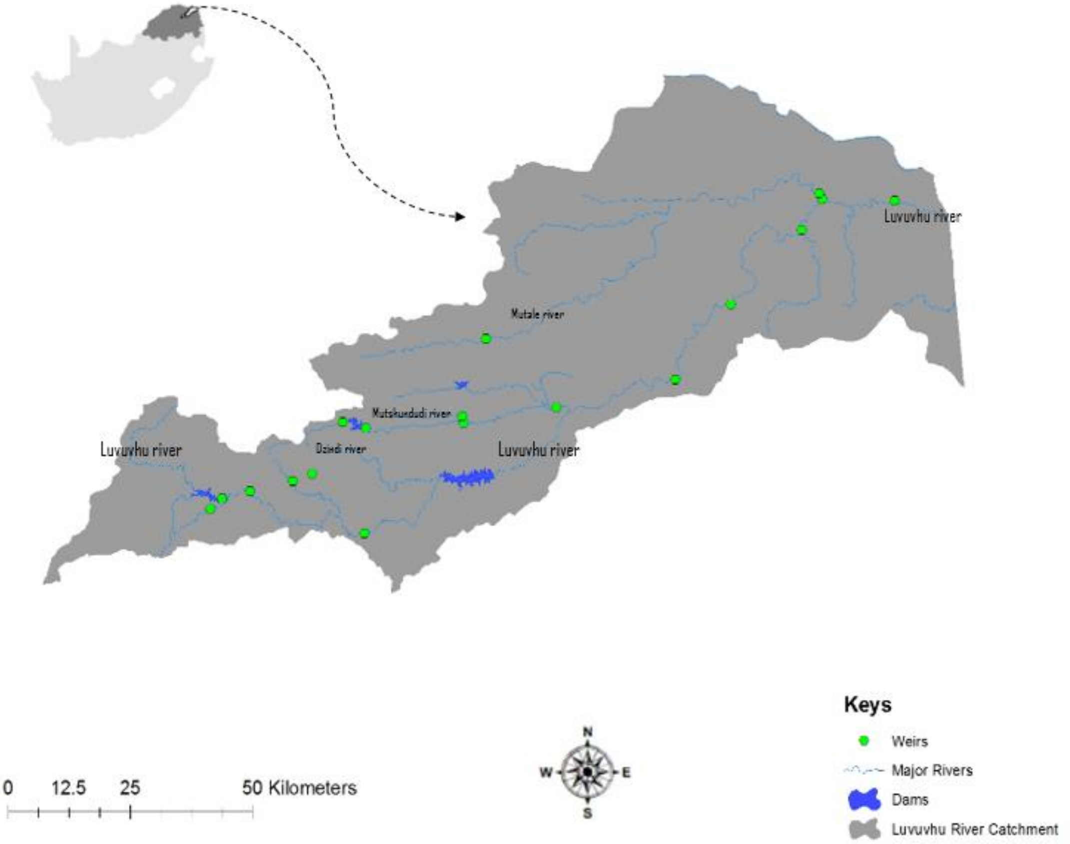

Figure 1.1: The Luvuvhu River catchment showing major rivers, elevation gradient and major villages. Insert map shows the location of the LRC in the map of South Africa.

The Luvuvhu River catchment (LRC) (Fig. 1.1) is located in the Luvuvhu-Letaba water management area, with a catchment size of approximately 5940 km^2. This catchment has 14 quaternary catchments (zones of homogeneous hydrological response, the smallest broadly accepted level in the order of catchment types), with the main river channels being the Luvuvhu, Mutale, Mutshindudi and Dzindi Rivers (Jewitt and Garratt, 2004). Long-term annual rainfall and air temperatures have not changed significantly over the last 100 years in both the lower (Kruger National Park) and the upper (Levubu) sections of the Luvuvhu catchment (Nkuna and Odiyo, 2016; Van Wilgen et al., 2016; MacFadyen et al., 2018). However, this catchment is currently subjected to major forms of stream flow alteration, including large dams and abstraction (Makhera et al., 2011; Kleynhans, 1996). The LRC is important to forestry, macadamia, avocado and banana plantations which are agricultural developments in the valleys of the headwaters (western side), and to rural and urban settlements and natural conservancy in the mid and downstream areas respectively (eastern side) (Angliss et al., 2001). The LRC rivers and riparian vegetation are home to many birds and animal species (DWAF, 2012; Evans, 2017), while the Luvuvhu River acts as a primary source of water in the northern parts of the Kruger National Park (Angliss et al., 2001). These rivers are also important because they directly support the Limpopo River which is an international shared water resource (Mwenge Kahinda et al., 2016). The LRC rivers together with their existing large dams (Nandoni, Albasini, Vondo, Holy forest, Damani, and Tshakhuma) and other 80 small agricultural dams are also used for a variety of recreational and subsistence purposes (Viljoen et al., 2011; DWAF, 2012). Large dams stores and hold a volume of water above the threshold of small dams (> 3 Mm^3) (Mantel et al., 2016). According to the most recent reliable census data, there are about 518 000 people in the LRC (DWAF, 2004). More than 90% of the population is classified as rural, most of whom live in rural villages and informal settlements, with the town of Thohoyandou rapidly developing and hosting most of the population (DWAF, 2004; Foord and Fouché, 2016).

1.7. Problem statement

Water managers are increasingly challenged to provide reliable and affordable water supplies to not only to growing human populations, also to the agricultural sector which is probably the largest water consumer (Nkuna and Odiyo, 2016). This has led to a decline in surface water resources in southern Africa increasing conflicts between different competing users such as agriculturalists and domestic users (Valimba and Mkhandi, 2005), a case in point for the LRC (Kleynhans, 1996; Ramulifho et al., 2019). With the current increase in both forestry or irrigation significantly reducing stream flow in the LRC (Jewitt et al., 2004), other aspects such as catchment mismanagement and the physical alteration of aquatic habitats are often likely to exacerbate the system's condition (Kleynhans, 1996). Studies show that conflicts over the most essential services of aquatic ecosystems, particularly rivers, between ecological and societal needs are increasing as global population and water demand rises (Bunn & Arthington, 2002; Nilsson and Renöfält, 2008; Poff et al., 2010). With the degradation of the quality and quantity of water in aquatic systems continuing to become a serious problem in rivers (Kleynhans, 1996), the assessment of biological and ecological response is therefore a critical aspect in riverine management (Dallas and Rivers-Moore, 2014). The goal behind these biological and ecological assessments is to negotiate for satisfactory tradeoffs in water allocation among all users of the resource and the resource base itself (the river or ecological integrity). In contrast to widely applied and expensive chemical assessments, biological assessments or indicators of water quality represent a cost effective, faster and easier alternative (Bauernfeind and Moog, 2000).

Much progress has been achieved in southern Africa over the past years to understand hydrological and biological health of rivers (Dallas, 2008; Kusangaya et al., 2013; Dallas and Rivers-Moore, 2014). However, reduction of stream flows is likely to result in a change in perenniality of rivers from permanent to non-perennial, while permanent wetlands becoming seasonal or temporary (Kleynhans, 1996). Some studies in the LRC recognize the need to limit both water abstractions and changes to the river flow regimes by setting environmental standards that guard and maintain river ecosystem characteristics and functions (Kleynhans, 1996; Jewitt and Garratt, 2004; Jewitt et al., 2004). While the Orange and Great Fish Rivers are amongst some of the most studied system in the country because of their problems of pest blackfly (Rivers-Moore et al., 2008; Rivers-Moore and Palmer, 2017), no study has evaluated the potential use of mayfly and blackfly as biological indicators in the Luvuvhu or for much of the north-eastern parts of South Africa.

1.8. Study aims

This study had three aims which are as follows;

(1) To quantify long-term changes in the stream flow regime of the Luvuvhu catchment.

(2) To assess the influence of environmental variables on both mayfly and blackfly assemblage structure in semi-arid rivers of the Luvuvhu catchment.

(3) To identify indicator species and change-point threshold of mayfly and blackfly species along important environmental gradients.

1.9. Structure of the thesis

The study consist of four main data chapters which address each of the aims above, while the fifth chapter (currently chapter 6) discusses the key findings of this thesis, provide a synthesis that would guide future work. These chapters are presented using paper formats and this might see the repetition of some sections of the chapters such as the description of the study area.

- Modeling stream flow trends using daily and sub-daily flow: evidence linking decrease in flow to seasonality and water abstraction in rapidly developing arid region of southern Africa.
- The role of hydro-environmental factors on Mayfly (Insecta, Ephemeroptera) community structure in the Luvuvhu River catchment, South Africa.
- Predicting blackfly diversity in the Luvuvhu catchment: stream flow consistently included in all models.
- Challenges to Implementing an Environmental Flow Regime in the Luvuvhu River Catchment, South Africa.

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Chapter 2: Characterization of sub-daily flow and long-term stream flow changes using daily flow data in a rapidly developing arid region of southern Africa

Abstract

As the impacts of the anthropocene intensifies in rivers, there is an increasing need to understand how these changes affect stream flow, one of the most influential drivers of spatial and temporal dynamics of stream biota. Impacts of flow are not only limited to altered quantities but also variability and timing. These changes are predicted to be disproportionately higher in southern Africa compared to most other regions of the world, highlighting the strategic importance of water resources as buffers. In this paper, flow in a strategic water resource area in an arid region of southern Africa was studied, exploring changes in stream flow over time, and the correspondence between daily and sub-daily flow metrics based on long-term flow data (85 years). The shape of flow duration curve (FDC) for the selected station was investigated in terms of its underlying process controls. The structure of the residual errors for most models pointed to altered flow regimes and only flow at one station was considered natural based on temporal autocorrelation. Trends showed a substantial decrease of 53% in stream flow and were most pronounced during the wet season, while water temperature is rising. Most of the sub-daily flow metrics were related to daily flow metrics. Variability in flow metrics have also increased over time, while FDC-based method indicated changes in streamflow patterns over time. Rainfall and temperature have remained the same over time, which suggest that declining stream flow might probably be linked to water abstraction related to commercial agriculture in the catchment. These declines in flow together with increased variability will have profound impacts on the instream aquatic biota.

Keywords

Catchment management; hydrological change; Limpopo Province; long-term flow; streamflow data; sub-daily flows.

2.1. Introduction

A primary goal in stream ecosystem assessments and management is to develop a suit of rules for managing stream flow regimes to attain some desirable level of river specific ecological functions (Richter et al., 1997; Poff et al., 2006). Globally, it is now recognized that catchment management and regulations on a regional scale should aim towards achieving well-functioning stream flow regimes for ecological integrity (Tharme, 2003). Stream flow is one of the most recognized and major abiotic determinant of spatial and temporal dynamics of plant, benthic and other taxonomic groups in streams (Bunn and Arthington, 2002). Earlier notions of minimum low flows in the maintenance of aquatic ecosystems have evolved to include a more comprehensive view of naturally variable stream flow regime (Arthington et al., 2006; Poff et al., 2010) Hydrological variability of streams are influenced by climate, physical characteristics of the catchment and human activities (Donald et al., 2004; Marengo, 2004; Omar et al., 2006; Zhang et al., 2017). Several approaches exist for analyzing stream flow variability (Tharme, 2003), and no clear consensus exists as to which variables amongst daily, seasonal, annual and inter-annual metrics are most relevant in aquatic integrity and management assessments (Poff et al., 2006). However, the statistical metrics used in the description of stream flow variability should be hydrologically and biologically significant (Colwell 1974, Richter et al., 1997 and Bevelhimer, 2015). Changes in stream flow variability have been shown to reduce abundance, diversity, reproductive success and survival of aquatic and riparian species (Zimmerman et al., 2010; Bejarano et al., 2017).

As water resource problems and water shortages related to current global climate change worsen, stream flow patterns and variability in extremes changes, increasing the number of water-related disasters (Bunn and Arthington, 2002; Poff and Zimmerman, 2010). These changes in the magnitude and frequency of extreme flow events have already been observed (e.g. floods and drought) (Kusangaya et al., 2013; Dallas and Rivers-Moore, 2014). Globally, pressure on water resources from increasing populations, irrigated agricultural development, and rising standards of living have drastically altered the already stressed hydrological flow regimes (Masih *et al.*, 2008). Valimba et al.,

(2007) argues that changes in surface water resources in Southern Africa reflect changes in rainfall in West Africa, while their severity is increased by human-related activities (e.g. land-use changes: urbanization, deforestation, changes in agricultural practices, engineering works, dam construction and river regulation) (Nyoni et al., 2013). Although there is evidence of increasing frequency of high rainfall and stream flooding events, past studies have identified a mixture of increasing and decreasing rainfall amounts in some parts of southern Africa with no strong evidence of declining or increasing trends (Burger and Du Plessis, 2007; Odiyo et al., 2015;Nkuna and Odiyo, 2016; Van Wilgen et al., 2016; de Waal et al., 2017; MacFadyen et al., 2018). In South Africa, several if not all, rivers are subjected to some major form of alteration and deterioration (Kleynhans, 1996).

Measures of stream flow variability are derived from time series, either by agglomerating or disaggregating data. Agglomerative approaches make use of techniques such as duration curves, while disaggregation approaches attempt to use descriptive statistics such as mean, range, standard deviation, and coefficient of variation to understand the links between timing, duration and magnitudes of stream flow regime (Richter et al., 1996, 1997; Rivers-Moore et al., 2013). Disaggregation has been widely used in hydrological assessments to understand flow variability (Richter et al., 1996, 1997; Taylor et al., 2003; Rivers-Moore et al., 2013; Bevelhimer, 2015). These metrics are derived from sub-daily (e.g. hourly interval series) data which may be summarized into daily statistics (mean, minimum and maximum). Daily flow data are widely available and used, although it is not yet generally clear if this captures key components of sub-daily flow variation which are principal drivers of ecological processes (Zimmerman et al., 2010; Bevelhimer, 2015). Sub-daily flow variation drives short-term habitat use (Bejarano et al., 2017), migration (Zimmerman et al., 2010) and spawning success (Grabowski and Isely, 2007). Empirical evidence also suggests that changes in the frequency, magnitude and predictability of sub-daily flow fluctuations reduce abundance, diversity and survival of aquatic species (Bevelhimer, 2015). High sub-daily flow fluctuations, such as that from hydro-electric schemes, can increase species stranding and displacement, altering taxonomic predation, and scouring fine sediments and macroinvertebrates (Haas, 2014).

Long-term (> 20 years) stream flow data offers valuable insights into drivers of streamflow as well as management options that might help rivers adapt to, or mitigate the impacts of climate and land use change on water abstraction (Medley et al., 2011). However, the length of records needed to detect a meaningful trend in stream flow inferences is problematic (Huh *et al.*, 2005), as the required time series length is governed by regional climate variability. Given limited availability of stream flow data, studies have defined both long-term and short-term analyses using temporal sequences of different lengths. Richter et al., (1996), Markovic et al., (2013) and Taylor et al., (2003) suggest the use of at least 20 years of consecutive stream flow records and a seven-year time scale to determine long-term inter-annual flow, whereas Huh et al., (2005) suggest at least 40 years of streamflow records may be necessary to adequately characterize long-term high-flow variability, and the World Meteorological Organization (1976) recommended a period of 30 years or longer as ideal for studies dealing with long-term changes. The study by Ahearn (2008) argues that any use of daily mean flow records of up to 10 years is referred to as short-term stations. To date, there is no consensus on the issue of the most appropriate length of data and the definition for long-term variability analysis.

Considerable progress has been achieved in Southern Africa to understand stream ecosystems integrity and stream flow variability concepts (Hughes and Smakhtin, 1996; Valimba et al., 2007; Kusangaya et al., 2013; Rivers-Moore et al., 2013; Dallas and Rivers-Moore, 2014). In some catchments, monitoring of temporal variables such as stream flow and other parameters of water quality has a long tradition, a case in point would be the 90 years of data for the Luvuvhu River catchment (LRC) as reported by Foord and Fouché (2016) and Heath and Classen (1999). Dam construction, water quality problems and water abstraction are the major cause of the deterioration of ecosystem integrity (Mwedzi et a., 2016; Kleynhans, 1996). However, there is no reported study that adequately takes into account temporal auto-correlation in the assessment of stream flow data for trends and duration curve analyses. What is also unclear for southern Africa is how sub-daily flow relate to daily flow, climate and catchment characteristics. With growing global emphases on sub-daily flow analyses (Bevelhimer, 2015; Zimmerman et al., 2010; Haas, 2014), it is important to evaluate how much hydrologic variation is explained by daily versus sub-daily statistics. This study therefore aimed to: (i) quantify changes in the stream flow regime over time at a catchment scale in the Luvuvhu River Catchment in South Africa; (ii) generate insights into factors that determine the shape of flow duration curves (FDCs) and (iii) explore the degree of hydrologic similarity between daily and sub-daily flow metrics.

2.2. Methods

Study site

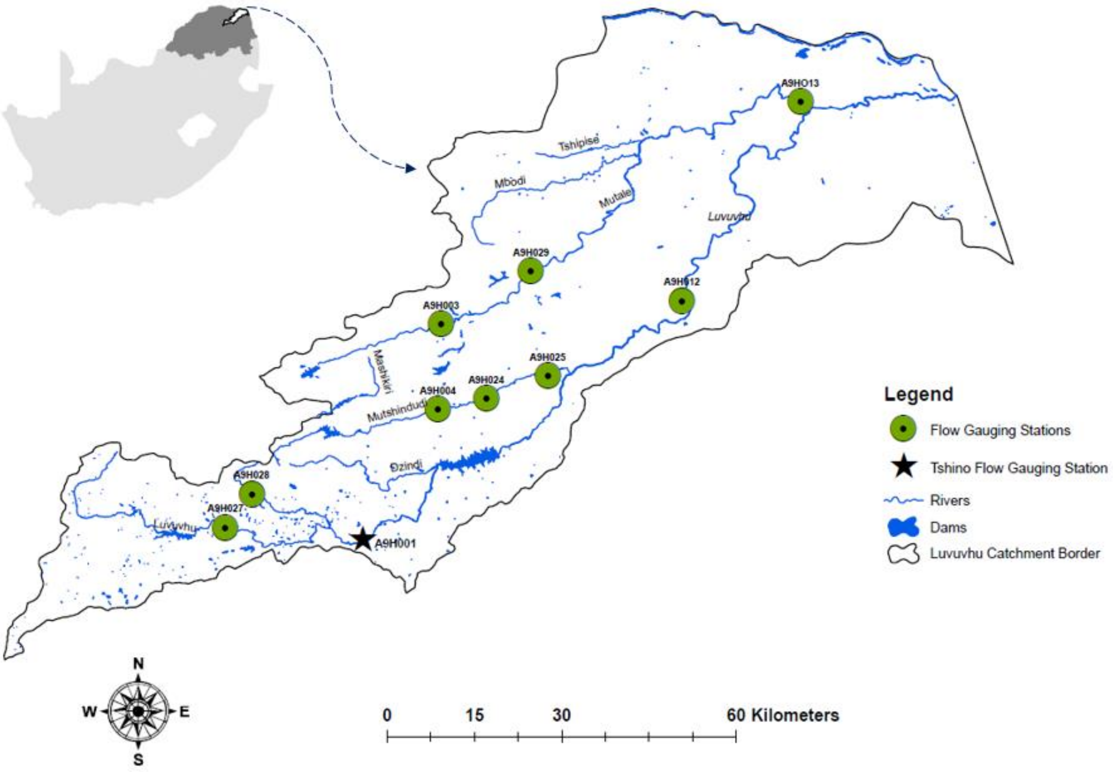


Figure 2.1: Map showing the locations of major rivers and streamflow gauging stations within the study area. Insert shows location of study region in the north eastern of both Limpopo and South Africa.

The LRC is located in the Luvuvhu-Letaba Water Management Area in the north eastern part of the Limpopo Province of South Africa (Fig. 2.1). The LRC represents a river which is significant both from a human and ecological perspective in a semi-arid region (Kleynhans, 1996). The LRC has an area of approximately 5 940 km^2, of which the lower 24% is protected in the Kruger National Park (KNP) (Heath and Classen, 1999; Jewitt and Garratt, 2004). The most geologically prominent feature of the catchment is the Soutpansberg Mountains, ranging from the east to west in the catchment (DWA, 2012). Elevation in the catchment varies from 1587 m altitude in the Soutpansberg Mountains to 200 m at the Limpopo River confluence in the east. The main river channel is the Luvuvhu River and, together with its tributaries (Mutshindudi and Mutale Rivers), deeply divides the basin (DWA, 2012). These main river channels begin the downstream journey in the highlands of the Soutpansberg Mountain flowing in an eastern direction through a range of landscapes and aquatic habitat types before joining the Limpopo River (Heath and Classen, 1990; Kleynhans, 1996; Angliss et al., 2001; DWA, 2012; Foord and Fouché, 2016). The plains consist of low-to-moderate relief, although open hills and low mountains with high relief are also present (Kleynhans, 1996). The geology of the Luvuvhu River catchment comprises three main groups of rock, namely the Basement Rocks (granitoid gneisses which underly most of the upper 80 km length of the catchment), the Soutpansberg mountainous area and the Karoo Sequence comprising sandstone, shale, grit, conglomerate and basalt in the lowlands of the catchment (DWA, 2012). Geology and relief define the land use in the catchment. Land use in the southern highlands of the LRC is dominated by exotic tree plantations of pines and eucalyptus and includes commercial forestry (4%), commercial dry land agriculture (10%), commercial irrigation agriculture (3%), range land (50%), conservation areas (30%) and urban areas (3%) (Jewitt and Garratt, 2004; Odiyo et al., 2015).

The overall climate of the LRC is classified as semi-arid, being largely driven by the topography of the area and with most of the rainfall occurring in December - February (Heath and Classen, 1990). Temperature increases from the mountains in the west to the plains in the east of the catchment. The mean annual air temperature of the Luvuvhu is between 20 to 22 ºC (DWA, 2012). The climatic condition of the catchment ranges from high rainfall humid areas in the mountainous northwest with a Mean Annual Precipitation (MAP) of 1 800 mm, to the low rainfall and hotter areas in the north-eastern lowlands of the catchment with a MAP of 400 mm per annum (DWA, 2012). The average MAP of the entire catchment varies between 610 to 800 mm due to high temporal and local climatic variation (Heath and Classen, 1990; Angliss et al., 2001; Jewitt and Garratt, 2004; DWA, 2012;). The mean annual evaporation of the Luvuvhu River catchment is 1 678 mm while the mean annual runoff (MAR) is 519 million m^3 (DWA, 2012). Changes in runoff have been recorded for a ninety-year period from 1900 to 1990, with periodic cessation in flow in recent times in some of the perennial streams (Foord and Fouché, 2016).

Gauging stations

Flow stations were selected across the catchment based on the availability of long-term (> 20 years) stream flow data (Table 2.1) to minimize the effects of inter-annual climatic variation on stream flow statistics and regime (Richter et al. 1997). Stations with instances where recordings had malfunctioned were removed from the data set and only stations with less than 10% of data missing were included in the analyses. Six of the ten gauging stations had long-term data (Table 2.1).

Stream flow data quality

Flow data from stations were assessed by visually inspecting time series plots and by estimating patterns in the temporal autocorrelation function (ACF) using the ‘acf’ function in R (R Core Team, 2019) and the 'DHARMa' package (Florian, 2018). Values of ACF at different time lags indicate whether there is any autocorrelation (Zuur et al. 2009) and values should have serial correlation between closely related days and serial correlation declines with time because stream flow at some future time is less and less likely to be the same as the current rate of flow (Yue at al., 2002).

Visual inspection of time series plots and subsequent regression of mean daily flow data calculated using more reliable sub-daily flow data (of 12 minute intervals), suggest that daily mean flow data is unreliable (Fig. S2.1, Table S2.1). Residual plots also suggest that flow at most of the stations is not natural. Both time series and residual plots data from Mhinga, Ngudza and Thengwe suggest controlled discharge events upstream (Fig. S2.2-S2.4). The long-term gauging stations at Thengwe, Ngudza and Tshino also only recorded flow less than 9 m^3/s before 1960 when recalibrations were done. However, this was not considered to have had a major impact on the results as high flows greater than 9 m^3/s since 1960 represent less than 2% of the total flows.

Tshino was the only gauging station with a temporal autocorrelation structure that reflect natural flow conditions, i.e. high serial correlation between closely related days (Fig S2.4) and for which we had sub-daily flow data for the whole period of the study. Therefore, only flow data from this gauging station was used when analyzing the long-term flow trends. However, since 2005, this station has not been operational (Table 2.1).

Table 2.1: Details of gauges in the Luvuvhu river catchment from the DWS database. Long-term stations indicated by the use of σ (* -Tshino). Temperature and rainfall stations are in italics.

Flow station number	**Station name**	**Data type**	**River**	**Lat (°S)**	**Long (°E)**	**Upstream dam**	**Period**	**Data Completeness (%)**	**Elevation (m)**	**Catchment Area (km^2)**
A9H001 *	Tshino	Flow	Luvuvhu	-23.11	33.38	Albasini	1931-2005	100.00	584	902
A9H003 σ	Ngudza	Flow	Tshinanne	-22.99	30.52	None	1931-2016	98.18	577	62
A9H004 σ	Thengwe	Flow	Mutale	-22.87	30.53	None	1932-2004	97.83	590	320
A9H012 σ	Mhinga	Flow	Luvuvhu	-22.86	30.88	Nandoni	1987-2017	92.45	427	1758
A9H013 σ	Kruger	Flow	Mutale	-22.43	31.07	None	1988-2017	81.83	273	1776
A9H024	Dzhingahe	Flow	Mutshundudi	-22.94	30.35	Thathe	1994-1999	98.95	550	51
A9H025 σ	Matsika	Flow	Mutshundudi	-22.85	30.68	Thathe	1996-2017	63.94	492	387
A9H027	Levubu	Flow	Lutanandwa	-23.05	30.23	None	2002-2018	98.21	708	46
A9H028	Nooitgedacht	Flow	Luvuvhu	-23.08	30.17	None	2003-2018	99.12	706	607
A9H029	Tshandama	Flow	Mutale	-22.77	30.77	None	2003-2018	99.12	592	329
0723485AO	*Levubu*	*Temperature*	*None*	*-23.08*	*30.28*	-	*1970-2004*	-	*670*	-
0723485AO	*Levubu*	*Rainfall*	*None*	*-23.08*	*30.28*	-	*1970-2004*	-	*670*	-

Prediction and verification of water temperature

There are no data on water temperature records for rivers in the LRC. Water temperature at Tshino station was then simulated using a multiple linear regression model developed by Rivers-Moore et al. (2005, 2008). This model incorporated daily stream flow and air temperature data to simulate mean daily water temperatures for South African rivers across a range of stream orders and altitudes (Rivers-Moore at al., 2008). This model was tested and validated by correlating between simulated and observed water temperature at two stream flow gauging stations in the LRC (Table S2.2). The correlation showed a positive and relatively stronger relationship between observed and simulated (Fig. S2.5)

Long term rainfall and air temperature data

Climatic data used in this study consist of monthly rainfall and temperature data from the Levubu weather station, 15 km east of Tshino weir, and for a period of 35 years (1970 – 2005) (Fig. 2.1). Daily rainfall and temperature data were provided by the South African Weather Service (SAWS). The rainfall and temperature records for this study had no missing data.

Long-term stream flow, water temperature, rainfall and air temperature trends

Linear models for stream flow were fitted to daily, 7-day maximum, 7-day minimum, monthly and annual time series data using Generalized Least Squares (GLS) to model temporal trends at Tshino. Trends in flow was then modelled by including an autoregressive (i.e. flow at a specific point in time depends linearly on its own previous values) and moving average (ARMA) error structure argument in the ‘gls’ function of the package ‘nlme’ (Pinheiro et al. 2014). Models were compared using the Akaike information criterion (AIC) and the model with the lowest AIC were retained. Linear regression models were fitted to mean monthly rainfall, water temperature and air temperature data using simple linear regression (SLR) to model temporal trends in long-term rainfall and temperature data. A positive value of the slope indicates an increasing trend and a negative value a decreasing trend. Linear regression patterns in the temporal trends were run using the ‘lm’ function in R.

Relationships between sub-daily flow and daily flow metrics

Sub-daily flow data, recorded at 12 minute intervals, between February of 2002 and April of 2006 at all the selected stations. Mean flow data was calculated from the sub-daily flow data. We then compared sub-daily flow to daily mean flow of the same stations using a suite of metrics proposed by Bevelhimer (2015). The sub-daily flow metrics include: daily minimum, daily maximum, daily delta, standard deviation, maximum hourly ramp rate, daily path length, daily standardized delta, rise and fall counts difference, coefficient of variation, standardized maximum hourly ramping rate, and Richards-Baker flashiness index, as defined in Table S2.3. The daily mean metrics suite included daily coefficient of variation, spread in daily flows one, spread in daily flows two, rise rate, and fall rate (Table S2.3). Relationships between these metrics were analyzed using Pearson's product-moment correlations.

Temporal clustering using K-means Analysis

The K-means analysis was used to identify hydrologically homogeneous periods of similar streamflow patterns or behavior at Tshino. Clustered groups therefore define behaviorally similar periods in terms of daily flow metrics (Dikbas et al., 2013). Long-term temporal trends in these metrics were then visualized using principal component analysis (PCA).

Flow duration curves

The flow-duration curves (FDC) of the groups identified using the clustering exercise were used to visualize the percentage of time that a given daily mean discharge is equaled or exceeded. Duration curve analyses can be used as a general indicator of hydrologic condition (i.e., wet versus dry and to what degree) and its shape reflects the characteristic response of a catchment to rainfall (Holmes et al., 2002). We calculated the number of daily flow values greater than or equal to the particular flow category. This value was then divided by the total number of flows to find the percent of daily flows greater than or equal to the highest flow in that category (Mohamoud. 2008). This term is called the exceedance percentage. Using this percentage convention, zero corresponds to the highest stream discharge in the record (i.e., flood conditions) and 100 to the lowest (i.e., low flow conditions). Flow exceedance percentage were categorized as follows: between 0-10% as high flows, moist conditions (10-40%), mid-range flows (40-60%), dry conditions (60-90%), and low flows (90-100%).

2.3. Results

Long-term stream flow, water temperature, rainfall and air temperature trends

Except for the month of August, the AIC for all the models that included ARMA error structures, were smaller than models without any correlation structure (Table 2.2). Results for models that included a correlation structure are therefore reported here. Trends in long-term streamflow were all negative, but were only significant for the months of December, January and February where flow decreased between 1 and 2 orders of magnitude faster than in any of the other months (Fig. 2.2, Table 2.2). There was also strong evidence for decreases in 7-day minimum and mean monthly flow but weak support for decreases in maximum flows (Fig. 2.3, Table 2.2). Daily mean water temperature changed upwardly and significantly between 1970 and 2003 (Fig. 2.4; Table 2.2). The last 35 years saw no significant change in either rainfall or air temperature in the catchment that feeds into Luvuvhu River before it reaches the gauging site at Tshino (Fig. 2.5, Table 2.2).

Table 2.2: Linear trends in flow during each month of the year, 7-day minimum, 7-day maximum and for the complete data set during 1931-2005 period at the Tshino gauging station using the default water year from Oct. 1 to Sept. 30 and for mean monthly rainfall and temperature for Levubu weather station (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Period	**Y (Intercept)**	**Slope**	**Standard Errors**	**p - value**	**AIC (Without correlation structure**	**AIC (With correlation structure)**
Jan	3.15	-2.60×10^{-4}	0.00	< 0.001***	377.80	364.16
Feb	3.20	-2.30×10^{-4}	0.00	< 0.001***	371.72	358.61
Mar	3.19	-15.00×10^{-4}	0.00	0.13	388.74	369.90
Apr	3.05	-3.75×10^{-5}	0.00	0.69	418.26	417.69
May	2.28	-2.25×10^{-5}	0.00	0.62	337.65	334.81
Jun	1.74	-2.70×10^{-5}	0.00	0.32	274.31	268.73
Jul	1.72	-6.50×10^{-6}	0.00	0.88	321.98	324.01
Aug	1.71	-7.11×10^{-6}	0.00	0.81	344.10	344.95
Sep	1.80	-2.62×10^{-6}	0.00	0.87	341.75	309.07
Oct	2.48	-3.03×10^{-6}	0.00	0.97	471.27	443.39
Nov	2.74	-8.85×10^{-5}	0.00	0.38	439.44	430.89
Dec	2.89	-2.00×10^{-4}	0.00	< 0.0001***	382.84	375.20
7-day Min	2.05	-9.90×10^{-5}	0.00	< 0.0001***	17878.35	11510.82
7-day Max	3.25	-5.00×10^{-5}	0.00	0.060	26660.07	25818.03
Mean monthly flow	2.49	-8.59×10^{-5}	0.00	< 0.0001***	4517.31	3928.47
Monthly rainfall	85.23	-0.00017	16.88	0.93	5150	5062.8
Daily mean water temperature	14.57	1.958×10^{-01}	3.617×10^{-02}	< 0.0001***	55563.19	53630.30
Mean monthly minimum air temperature	15	0.42×10^{-4}	0.4 × 10-4	0.3	1987.3	1681.8
Mean monthly maximum air temperature	26	0.25×10^{-4}	0.5×10^{-4}	0.6	2238.2	1425.2

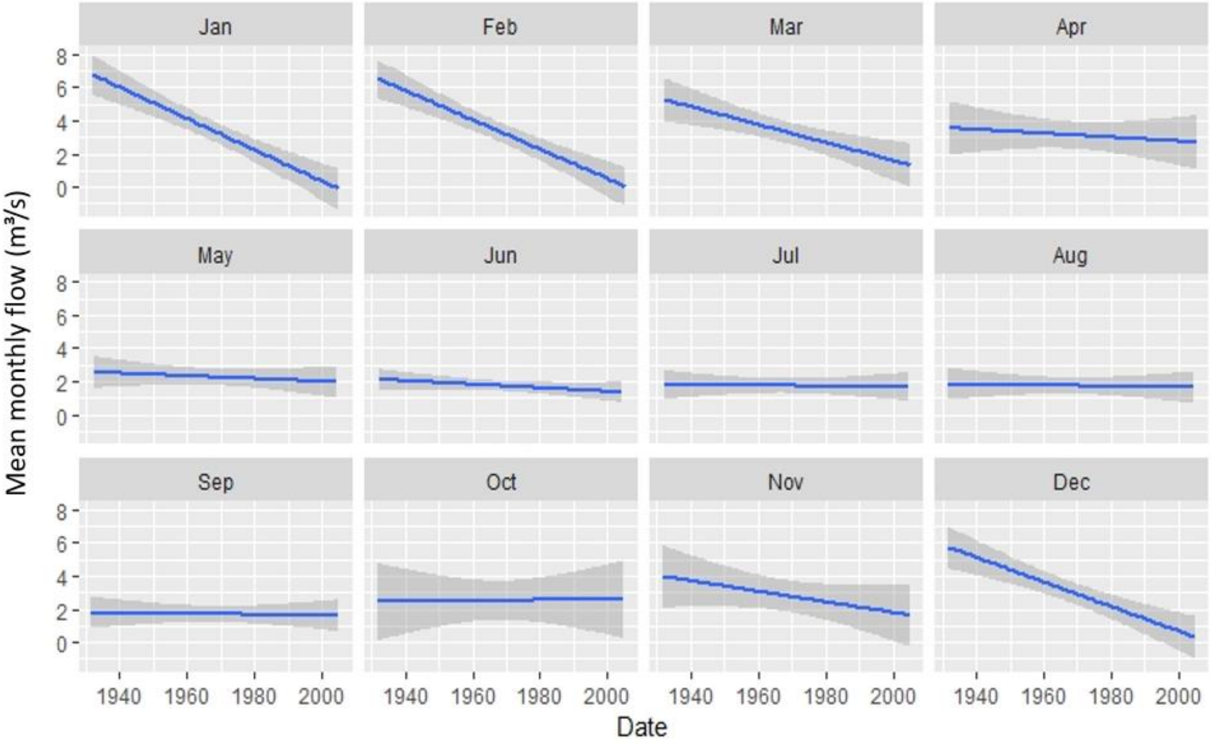


Figure 2.2: Fitted regressions of time series of streamflow at Tshino for each of the twelve months. The grey band represent 95% confidence intervals for streamflow.

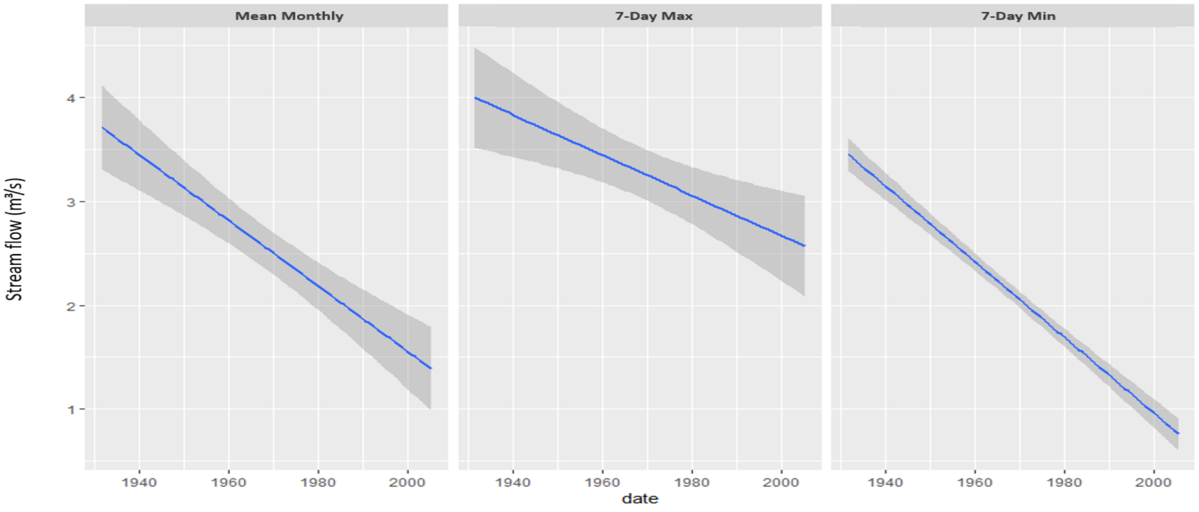


Figure 2.3: Fitted regressions of streamflow time series at Tshino for mean monthly, 7-day maximum and 7-day minimum metrics. The grey band represent 95% confidence intervals.

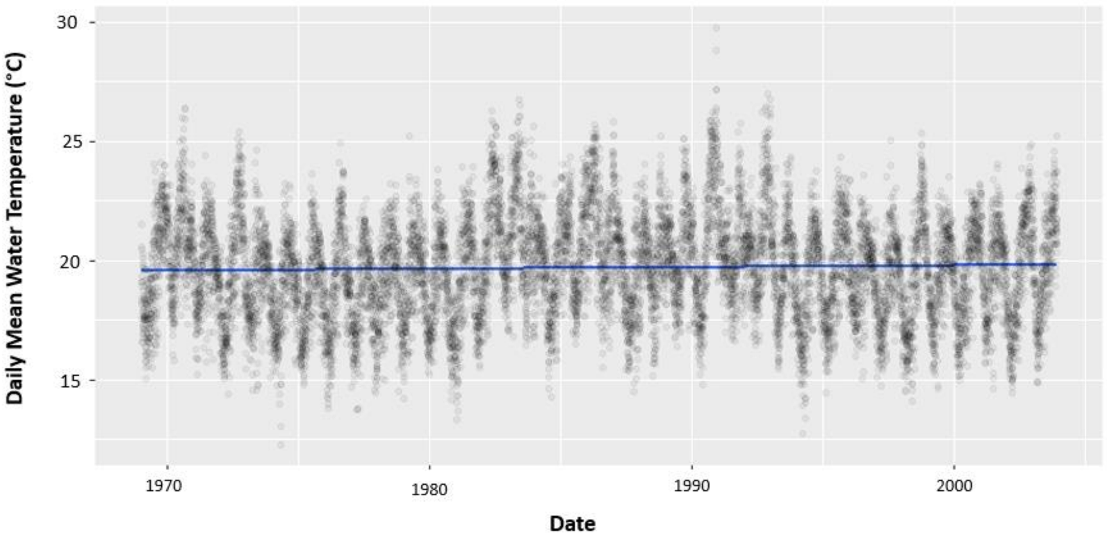


Figure 2.4: Time series (1970 – 2003) plot of daily mean water temperature for Tshino.

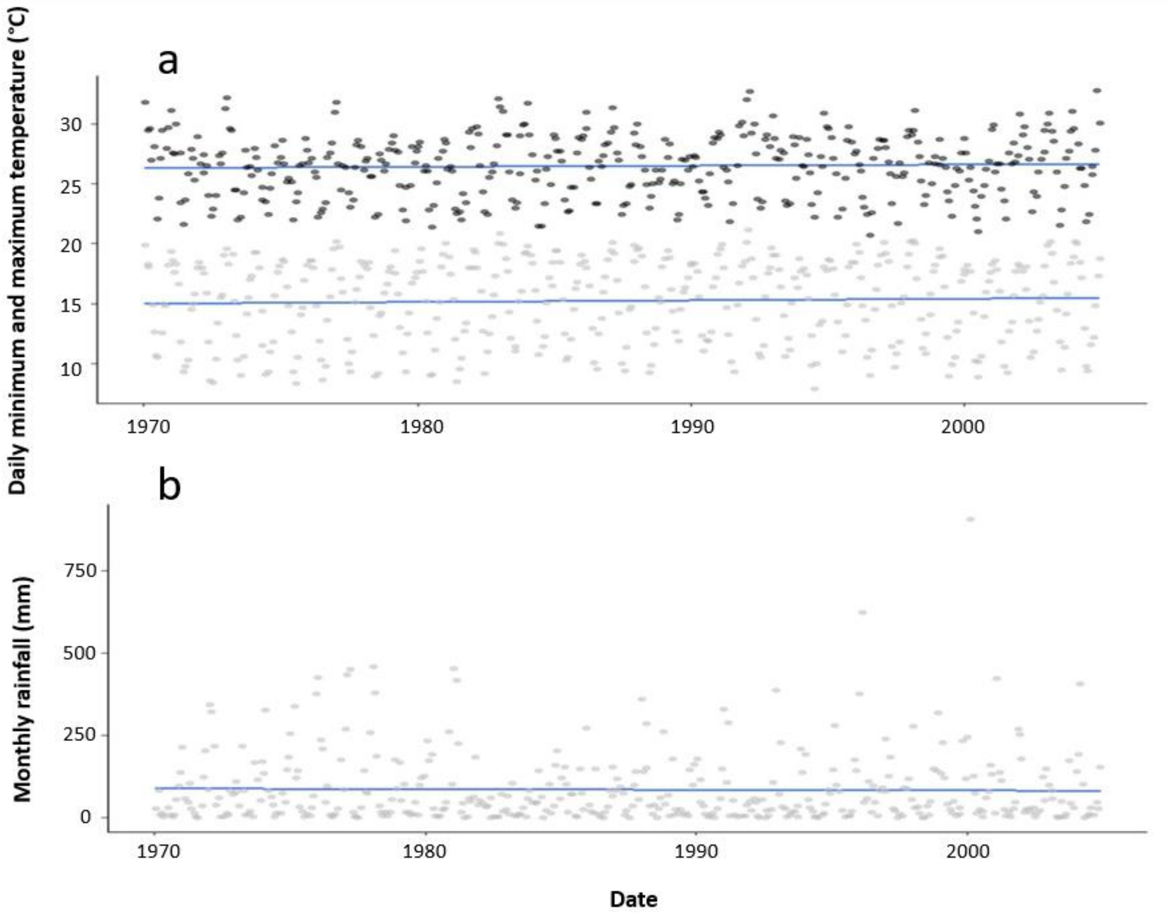
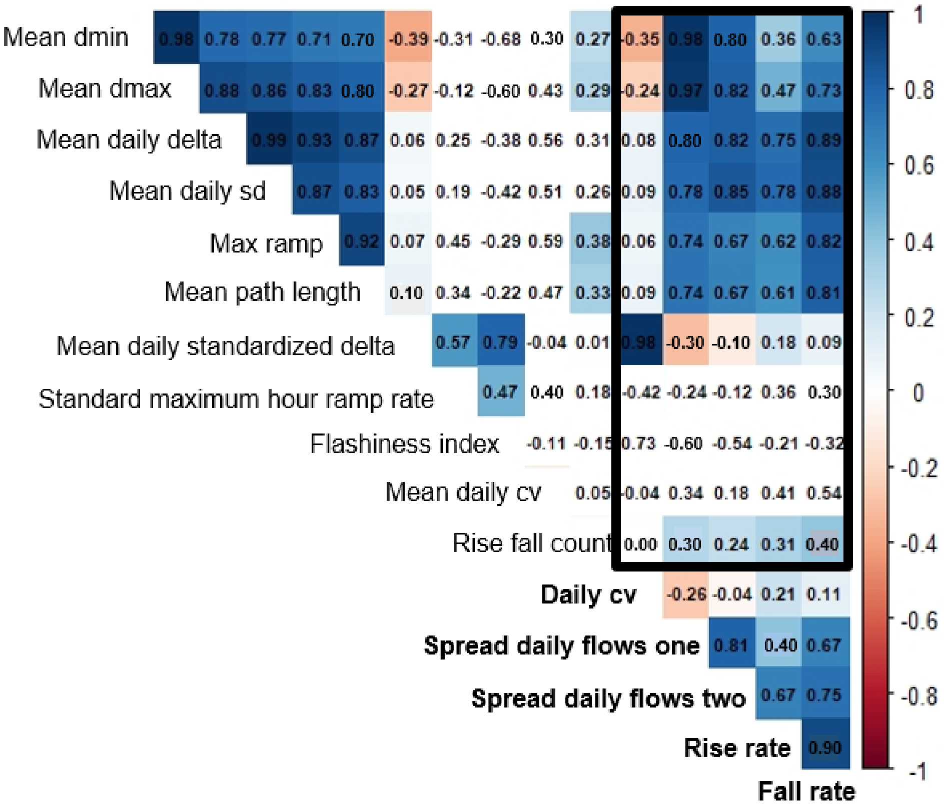


Figure 2.5: Time series (1970 – 2004) plots of (a) air temperature and (b) rainfall for Levubu weather station (15 km west of Tshino).

Relationships between sub-daily flow and daily flow metrics

The nature of correlation between sub-daily flow and daily flow metrics ranged from relatively strong (> 0.98) to weak (< -0.60) relationship (Fig. 2.6). About 78% of the coefficient of determination included cases where the correlation was positive as opposed to negative correlation. The daily flow metrics that showed zero or no correlation to sub-daily flow metrics included that of daily coefficient of variation and rise and fall count. Weak relationship (< ± 0.5) included relationship between daily coefficient of variation (daily) and the following sub-daily flow metric, mean path length, the maximum ramp rates, mean daily standard deviation and mean daily delta (Fig. S2.6). The correlation between spread in daily flows two and mean daily standardized delta, and mean daily standardized delta and fall rate were also weak (-0.1 to 0.09). Several metrics of daily and sub-daily flow showed relatively strong positive and significant relations (Fig. 2.6, Fig. S2.6). These included correlations between daily coefficient of variation, mean daily standardized delta, spread in daily flows one (daily) and both mean daily minimum and maximum. However, the strongest negative correlation (> - 0.5) included spread in daily flows one and spread in daily flows two (daily) and one metric of flashiness index (sub-daily).



	Mean dmax	Mean daily delta	Mean daily sd	Max ramp	Mean path length	Mean daily standardized delta	Standard maximum hour ramp rate	Flashiness index	Mean daily cv	Rise fall count	**Daily cv**	**Spread daily flows one**	**Spread daily flows two**	**Rise rate**	**Fall rate**
Mean dmin	0.98	0.78	0.77	0.71	0.70	-0.39	-0.31	-0.68	0.30	0.27	-0.35	0.98	0.80	0.36	0.63
Mean dmax		0.88	0.86	0.83	0.80	-0.27	-0.12	-0.60	0.43	0.29	-0.24	0.97	0.82	0.47	0.73
Mean daily delta			0.99	0.93	0.87	0.06	0.25	-0.38	0.56	0.31	0.08	0.80	0.82	0.75	0.89
Mean daily sd				0.87	0.83	0.05	0.19	-0.42	0.51	0.26	0.09	0.78	0.85	0.78	0.88
Max ramp					0.92	0.07	0.45	-0.29	0.59	0.38	0.06	0.74	0.67	0.62	0.82
Mean path length						0.10	0.34	-0.22	0.47	0.33	0.09	0.74	0.67	0.61	0.81
Mean daily standardized delta							0.57	0.79	-0.04	0.01	0.98	-0.30	-0.10	0.18	0.09
Standard maximum hour ramp rate								0.47	0.40	0.18	-0.42	-0.24	-0.12	0.36	0.30
Flashiness index									-0.11	-0.15	0.73	-0.60	-0.54	-0.21	-0.32
Mean daily cv										0.05	-0.04	0.34	0.18	0.41	0.54
Rise fall count											0.00	0.30	0.24	0.31	0.40
Daily cv												-0.26	-0.04	0.21	0.11
Spread daily flows one													0.81	0.40	0.67
Spread daily flows two														0.67	0.75
Rise rate															0.90

Figure 2.6: Heatmap of correlations between sub-daily and daily hydrologic flow metrics. The rectangular block represent the correlations between sub-daily flow and daily flow metrics. Daily flow metrics are in a bold block.

Hydrologically homogeneous periods

The first two principal components explained more than 90% of cumulative variation in the daily flow metrics at the Tshino gauge. From these variations, k-means cluster analysis identified four groups of hydrologically homogeneous periods (Fig. 2.7). Group 1 included years at the start of the time period (1930-1950). Flow metrics in this group are characterized by lower variability in flow and slightly higher flow than that of Group 3 and 4 (Fig. 2.7). Groups 2 and 3 (1960-1980s) are characterized by lower flow, while Group 4 (mainly 1990s and early 2000s) are related to increased variability and rise rates, the latter is probably related to flash floods. The y-axis is negatively related to coefficient of variation in flow and it is clear that the more recent dates (Group 4) are associated with increased variability. The time periods associated with the negative axis of PC1 corresponds to periods of extreme droughts in the region (Group 1 and 3), in particular the droughts of 1980's and

1990s. During these periods, daily mean, flow spread and high flood flow decreased with an increase in fall rate. Generally, it is clear that during the earlier period 1930-1960, metrics were much less variable, between and within years, as both coefficient of variation and standard deviation declined.

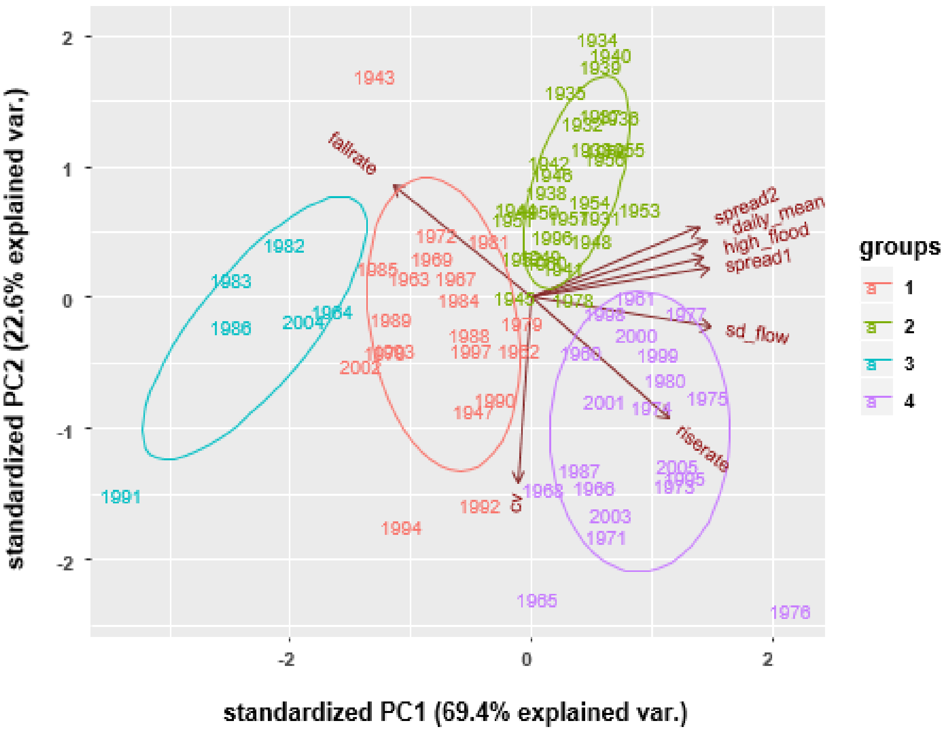


Figure 2.7: Principal component analysis of flow groups (PC axes 1-2) (showing flow metrics which were best correlated with flow groups) at Tshino.

Flow Duration Curve

The general shape of the curve for all groups shows a steep slope at the upper end, and a gradual decline in the middle, to a sharp dip at the lower tail, except for group 2 which had a steep and flat curve during high flows period (upper left end) (Fig. 2.8). However, group 1 and 3 had the lowest stream discharge rates in the record during all flow categories comparatively. Generally, group 2 and 4 had the highest flow rates, with the moist flow category (10-40%) ranging between 2.4 to 8m^3/s, while mid-range flows (40-60%) covers 1.3 to 2.4 m^3/s. Dry conditions (60-90%) had flow between 1 and 0.36 m^3/s for all the groups. The low flow category recorded flow of not greater than 1m^3/s for all groups, with large period stream flow cessation for group 3 relative to group 1 (Fig. 2.8).

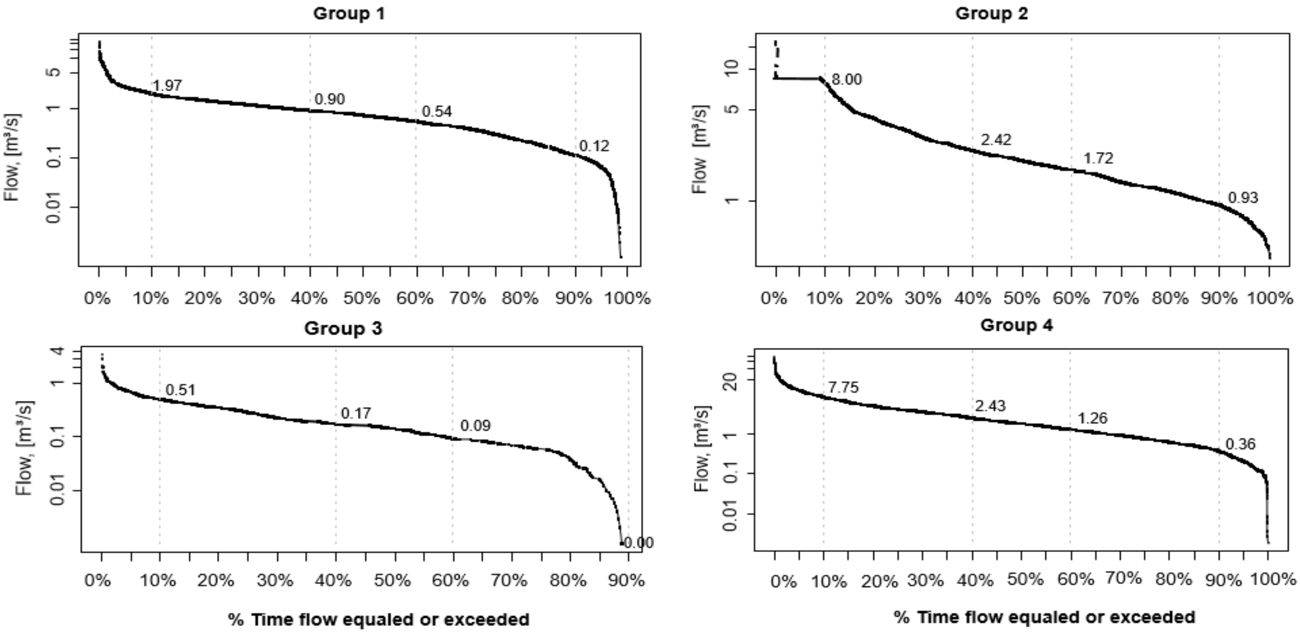


Figure 2.8: Flow Duration Curve for the Luvuvhu River at Tshino showing exceedance probability of the mean daily flow.

2.4. Discussion

Stream flow data quality

This study highlights the scarcity of quality flow data for the region. Except for one, all the gauging stations showed some form of flow regulation pointing to regular controlled releases upstream that has probably altered flow regimes considerably. Flow monitoring at most long-term gauging stations stopped around the year 2005. The lack of recent records are unfortunate and prevents meaningful evaluations of the stream flow impacts in these rivers. Jewitt et al. (2004) argues that proper modelling in water resources requires high level confidence in the model’s inputs and output data for accuracy and correctness in decision making. Errors in flow gauge data are sometimes due to sediment build-up on stage measurement, downstream submergence, and human and gauge calibration errors related to exceedances for high flows (Wessels and Rooseboom, 2009). Regular inspections, and the introduction of new gauging stations might provide for an improvement in data quality.

Long-term trends

Changes in stream flow regimes may result from a variety of factors, but is mainly related to climatic parameters (precipitation, temperature, evaporation) (Kusangaya et al., 2013). The declining stream flow trend in this current study is consistent with the findings of Odiyo et al. (2015), who noted that stream flow volumes in the Luvuvhu River have declined over the past 80 years. However, the increasing variability of stream flow regime in this study also corresponds to increase in climatic seasonality, with longer dry periods (Van Wilgen et al., 2016) and highly variable nature of rainfall (Odiyo et al., 2015). As also found in this study, majority of rivers in southern Africa are on an upward thermal trajectory (Kruger and Shongwe, 2004; Kusangaya et al., 2013). However, this study's analysis of 40 years rainfall and temperature data in Levubu, 15 km upstream of the flow gauge used for this study, found no significant changes in rainfall and temperature with time have been observed in the LRC, as also found by other studies (Nkuna and Odiyo, 2016; Van Wilgen et al., 2016). MacFadyen et al., (2018) also found that long-term annual rainfall has not changed over the last 100 years in the Kruger National Park, a large regional reserve overlapping the Luvuvhu catchment. Stream flow regime is driven by both rainfall and topography in the LRC (Odiyo et al., 2015), making the declining stream flow volume unexpected and surprising since it is not consistent with the climatic conditions of this region. Air temperatures have also not increased suggesting that possible losses because of increased evapotranspiration could not be ascribed to temperature changes in the catchment above Tshino to experience high evapotranspiration (Kleynhans, 1996; Hope et al., 2004). This decrease in stream flow may be linked to anthropogenic changes in land and water use (Valimba et al., 2007). Jewitt et al. (2004) highlighted the negative impact that commercial forestry and crop irrigation on runoff in the LRC and Kleynhans (1996) noted the extensive system of interlinking canals and modern first world farming methods had already started to drain a total of 15.4 million m^3/year of minimum stream flow to irrigate 1 845 ha of agriculture activities from the Luvuvhu and Latonyanda Rivers by 1987. We expect this number to have doubled, given the current transitioning to intensive commercial agriculture in the catchment (Evans, 2017). Some studies also link decreasing flow to channel bank storage (Beck et al., 2013), while others to evaporation (Abebe and Foerch, 2006; Fan et al., 2013).

The weak decline of stream flow during drier and cooler periods (April – September) of flow less than 1 m^3/s in the Luvuvhu could be as a result of inputs from channel bank storage and reduced evapotranspiration rate. Because the slope of the upper catchment of the Luvuvhu River is steep, this suggest that dry period stream flow is not just climate-drive, but is also controlled by permeable topography of soils forming on steep slopes which is often more permeable and promote base flow contributions relative to less permeable soils of gentle slopes (Beck et al., 2013). Regardless of the cause, the reduction in the volume of water in the Luvuvhu River in the upper reaches is a major threat to the catchment organisms whose lives are depend on stream flow (Kleynhans, 1996; Hope et al., 2004).

Flow Duration Curve

Aquatic habitat conditions are often correlated with discharge, and flow duration curve can be used to associate flow exceedance probability with transformation or stagnation of habitat conditions and aquatic organisms (McKay and Fischenich, 2016). The shape of flow duration curves presented in this study showed a generally declining magnitude of flow discharge from a steep high flow slope to sharp drop of flow. Holmes et al., (2002) argues that FDC with a high steep slope of higher flow magnitude throughout indicates a highly variable stream whose flow is largely due to quick stream flow discharge, while topography of the catchment (geology, geomorphology, soils, flow regulation by dams and diversions) (Hughes and Smakhtin, 1996; Mohamoud, 2008) and extraction of water by vegetation (McKay and Fischenich, 2016) along the stream banks affect low flows in the middle part and sharp dip at the lower tail of the duration curve respectively. Hughes and Smakhtin (1996) also argued that the increase in flow aridity in the lower tail of the FDC is largely driven by the existence abstractions from irrigation. In this study, this might be true for Tshino considering the amount of water abstraction at the upstream section of the station where large about of water is used for commercial irrigation (Hope et al., 2004, Foord and Fouché, 2016). However, because of complex interactions between climate and catchment physiographic characteristics that contribute to the generation of runoff by many different mechanisms, there is still a lack of comprehensive understanding of the relative contributions of all the drivers to the shape of FDCs (Yokoo and Sivapalan, 2011).

Relationships between sub-daily flow and daily flow metrics

A total number of 78% of sub-daily flow metrics were related to daily flow metrics. However, some of the correlations coefficients were small (< 0.75) which are consistent with the findings from Bevelhimer (2015) and Zimmerman et al., (2010), who noted that flow variability based on daily mean flow data were not sufficient to characterize sub-daily flow patterns. The majority of the relationships were highly significant (Fig. 2.6 & Fig. S2.6). This suggests that daily flow metrics can be used as a surrogate for some of the sub-daily metrics. These include daily standardized delta and both mean daily minimum and maximum flow. These metrics are of influence to feeding, spawning success, and recruitment of aquatic organisms (Haas, 2014; Bejarano, 2017). The lack of a good daily flow metric surrogate in relation to rise and fall count could negatively affect our ability to predict stranding events of aquatic biota and an overall decrease in aquatic biodiversity (Baker et al., 2004; Zimmerman et al., 2010). Changes in rise and fall rates and counts are mostly an outcome of the change in flow release operations and flow regulation (Haas, 2014). The sensitivity of biological organisms to sub-daily changes may lead to substantial loss of species in the fluvial systems. Sub-daily flow is therefore necessary to characterize the hourly or sub-hourly flow regime along a river reach (Bejarano, 2017).

Rise rate and the coefficient of variation increased in the latter part of the flow period, while mean daily flow decreased. These increasing stream flow variability and declining stream flow volumes could be related to increasing water abstraction and climate variability (Kleyhans, 1996; Van Wilgen et al., 2016; MacFadyen et al., 2018). Compared to the lower reaches which include the Kruger National Park and upper reaches where commercial agriculture is practiced extensively, the middle reaches of the Luvuvhu River have been the least prioritized zones as far as catchment management is concerned (Warburton et al., 2012). Another study by Kleynhans (1996) indicated that subsistence farming and management practices such as removal of riparian vegetation, erosion and sedimentation have reduced stream flow volume these areas.

Implications for aquatic organisms

With the decrease in natural flow volumes over the past 80 years and predicted flow cessation within in the next 15 years (Fig. 2.3, table 2.2) that mainly impact the hot rainy season in the region. There has also been an increase in the variability of flow over time. These changes will lead to increased extremes in daily flow metrics which will translate into increased sub-daily flow variability. These continued changes to the flow regime raise important concerns around the responses of aquatic biota. Foord and Fouché (2016) found a decrease in high flow intolerant taxa in the catchment possibly linked to the increased occurrence of extreme event while the abundance of stream flow generalist taxa remained unchanged. More studies need to focus on the ecological responses of aquatic communities to specific types of flow alteration in order to identify biodiversity threats, habitat change and design approaches for conservation planning (Dallas and Rivers-Moore, 2014).

2.5. References

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Chapter 3: The role of hydro-environmental factors in Mayfly (Ephemeroptera, Insecta) community structure: identifying threshold responses

Abstract

Freshwater organisms are threatened by changes in stream flow and water temperature regimes due to global climate change and anthropogenic activities. Threats include the disappearance of narrow-tolerance species and loss of thermal habitats for cold-adapted organisms. Mayflies are abundant and diverse benthic invertebrate that perform important functional roles and acts as indicators of river health. The relative role of key hydro-environmental factors such as water temperature and flow volumes in structuring these communities have rarely been explored in the tropical regions of Africa. Here we investigate the response of mayfly species diversity to these factors in the Luvuvhu catchment, a strategic water resource area in the arid north-eastern corner of South Africa. Mayfly larvae were sampled monthly in rheophylic biotopes across 23 sites over a one-year period. We found that temperature was the most important variable structuring mayfly assemblages. Five out of six reliable mayfly species were cold-adapted indicator species, with community threshold response to temperature at 19 °C. Results support laboratory-based thresholds of temperature for mayfly species survival and development, extending empirical evidence to include field-based observations. Increased global (climate change) and local (riparian vegetation removal, impoundments) changes are predicted to have negative impacts on mayfly diversity and ultimately on ecosystem function.

Keywords: Global climate change, Luvuvhu River catchment, South Africa, Stream flow, Thermal change, Threshold analysis, Water temperature.

3.1. Introduction

Freshwater ecosystems cover less than 1% of the Earth's surface, but provide a home to 10% of all known animal species, 60% of which are aquatic insects (Dijkstra et al., 2014). Natural flow and thermal regimes of these systems are increasingly threatened by anthropogenic activities which include habitat fragmentation, removal of riparian zones, eutrophication, abstraction, pollution, as well as global climate change and its associated increase in drought and flood frequency (Olden and Naiman, 2010; Dallas and Rivers-Moore, 2014). Rivers in particular, hold the highest proportion of benthic organisms threatened by climate change, influencing and altering assemblage structure, resulting in a loss of species diversity and ultimately altering ecosystem function (Bunn and Arthington, 2002; Dallas and Rivers-Moore, 2014).

Mayflies (Ephemeroptera) are a major component of these aquatic insect communities, with aquatic nymphs that are extremely diverse in shape and structure, reflecting their highly diverse habitats, locomotion, and feeding behavior (Baptista et al., 2006; Sartori and Brittain, 2015). They are ubiquitous in every kind of freshwater ecosystem (Buss and Salles, 2007; Alhejoj et al., 2014), representing the largest purely aquatic invertebrate order in streams and rivers (Dijkstra et al., 2014), while decreasing in lakes and ponds (Barber-James et al. 2008). Taxonomically, mayflies are relatively well studied (Dijkstra et al., 2014), with their entirely aquatic nymphs, representing the longest developmental stage in the life cycle of these organisms (Barber-James, 2016). Mayflies are distributed worldwide with over 3000 species, in more than 400 genera and 42 families (Barber-James et al. 2008).

Mayfly distribution is largely related to substrate type, water velocity, depth, turbulence, temperature and hydraulic parameters (Buss and Salles, 2007; Gustafson 2008; Vilenica et al. 2018), which are in turn influenced by a river's thermal and flow signature (Rivers-Moore et al., 2013). Water temperature and flow are major variables driving river ecosystems (Poff and Zimmerman 2010; Dallas and Rivers-Moore 2014) and mayfly assemblage structure in running waters (Pardo et al., 1998; Gustafson 2008; Nelson and Lieberman, 2002; Vilenica et al., 2017b;). This is because mayfly are ectothermic, and their fitness and physiology depends on flow and temperature for both their dispersal and development. (Hawkins and Hogue, 1997; Chessman, 2012). Oxygen availability, stream size, competition for food and space, resource availability, water chemistry and light provide finer scale filters of community assembly (Brooks et al. 2005; Finn and Poff 2005; Svitok 2006; Christidis et al. 2017), while human activities now impact mayfly communities at various scales (Klonowska-Olejnik and Skalski 2014) through flow regulation (Bunn & Arthington 2002), the removal of riparian forest (Siegloch et al., 2014) and bank degradation for agricultural activities (Allan 2004).

Mayfly species play a fundamental functional role in stream ecosystems as being consumers (filterers, collectors, predators and shredders) and prey at intermediate trophic levels and thus serving as channels by which bottom-up and top-down forces are transmitted (Wallace and Webster, 1996; Baptista et al., 2006). Mayfly community and structures of other functional feeding groups change as streams grow wider together with continuous gradient of physical variables downstream from springs to rivers (Vannote et al. 1980). This approach has been widely successful in the temperate streams (Masese et al, 2014), with little known for tropical systems (Boyero et al., 2009). Besides the fact that mayflies are especially diversified in temperate piedmont areas (Sartori and Brittain, 2015), the river continuum concept of predictable change of aquatic organisms downstream is difficult to apply in many tropical streams, with increasing evidence that related species occurring in tropical areas and other regions do not share the same diets (Masese et al, 2014). Even within regions, some taxa can shift their feeding in response to changes in land use and riparian conditions (Masese et al, 2014).

Mayfly community distributions can therefore reflect thresholds points and stress zones along an environmental gradient over space or time at which communities experience regime changes (Klonowska-Olejnik and Skalski 2014; Costas et al. 2018). Knowledge of mayfly community composition, seasonal dynamics, distribution, and their narrow habitat sensitivity extends their utility value from indicators and surrogates of habitat change (Bauernfeind and Moog, 2000; Vilenica et al., 2017a) to their inclusion as agents for adaptive and holistic conservation planning of running waters (Ramulifho et al. 2018). The choice of mayflies in river monitoring programs lies in the low cost of sampling associated with their collection and their high sensitivity level to water quality parameters (Snyder et al., 2014).

The Luvuvhu River catchment is a strategic water resource area (Nel et al., 2013) in the north-eastern arid region of South Africa. Flow in the catchment has experienced substantial decrease (> 53%) in stream flow volume over the last 80 years with a predicted flow cessation within the next 30 years (Ramulifho et al., in Review). The literature on the relationships between hydro-environmental variables and assemblage structure of aquatic organisms is limited for Afrotropical streams, particularly for the northern regions of South Africa, and is largely restricted to rapid biological assessments (Foord and Fouché, 2016). Here, we explore the relationship between stream flow, water temperature, and other important local environmental variables that drive assemblage structure in the Luvuvhu catchment. We aim to 1) describe mayfly community composition in the five major tributaries of the catchment, 2) explore the role of hydro-environmental variables, particularly flow and temperature, in explaining mayfly diversity, and 3) identify threshold responses to key drivers identified in the previous objective.

3.2. Methods

Study area

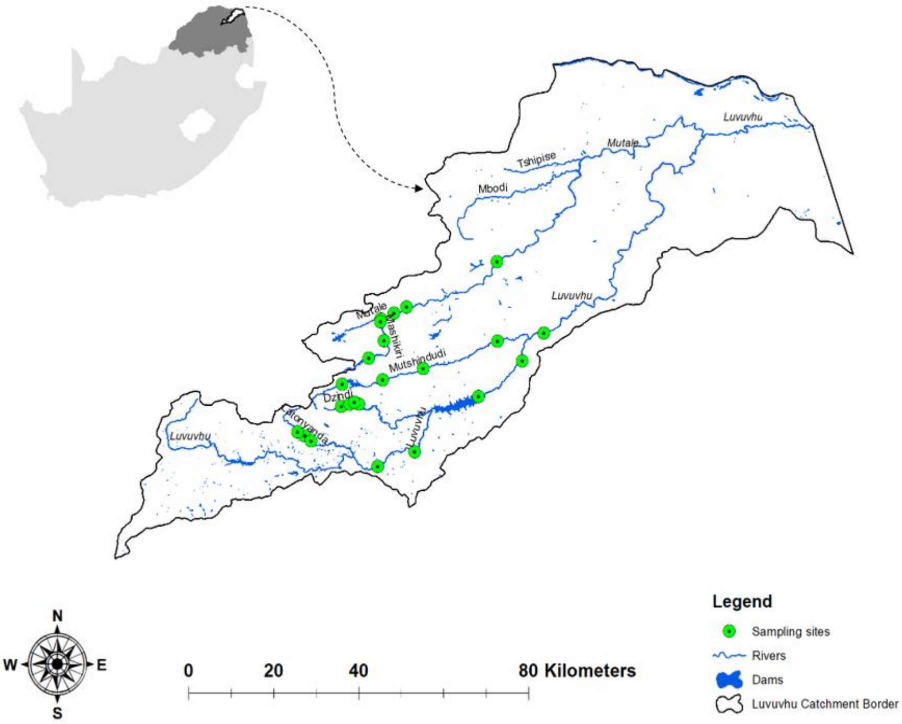

Figure 3.1: Location of sampling sites in the Luvuvhu catchment, Limpopo province, RSA. Insert shows location of study region in both Limpopo and South Africa.

The Luvuvhu River catchment (Fig. 3.1) covers an approximate area of 5 940 km^2, with a mean annual precipitation (MAP) of 608 mm, mean annual runoff (MAR) of 519 million m^3 (ranging from 85 to 1 900 million m^3) and an elevation range between 232 and 1587 masl (DWAF, 2012). Kleynhans (1996) classified streams in the Luvuvhu River as fairly natural, but recent agricultural intensification and the expansion of human settlements have had substantial impacts on instream biota (Foord and Fouche, 2016), and the flow regime has consequently been altered considerably (Ramulifho et al., In review).

Ephemeroptera sampling

Twenty-three sites (Fig. 3.1; Table S3.1) across six perennial streams in the Luvuvhu catchment were sampled based on the presence of a hydraulic biotope of shallow running water with large stones (10-

30 cm diameter). Mayfly diversity peaks in stony substrates (Christidis et al. 2017; Vilenica et al., 2017b). Initially, fourteen sites were sampled monthly to complete an annual cycle (December 2016 -January 2018), and an additional nine sites were included for the period between April 2017-January 2018 to allow for increased representation of environmental gradients. During each of the monthly surveys, six stones in each site were rinsed and brushed to dislodge organisms, and trapped downstream in a sampling net (30 × 30 cm; 250 µm mesh). Contents of the net were emptied into a sample bottle and sorted in the laboratory. All specimens were identified to the highest taxonomic level possible using de Moor et al. (2003). Identifications were subsequently confirmed by mayfly taxonomists (Dr. Helen James and Dr. Terence Bellingan) at the Albany Museum, South Africa. The organisms were preserved in 70% alcohol and deposited in a reference collection of benthic macroinvertebrates, at the University of Venda, South Africa.

Environmental variables

Instantaneous measurements for flow depth and flow velocity above each of the six stones were recorded using a Flow Globe FP101 (Global Water), while instantaneous readings for pH, water temperature (WT), total dissolved solids (TDS), and electrical conductivity (EC) were measured using portable multi-parameter water transmitters ‘Crison pH/mV’ (Table S3.1). The channel width at each sampling point was measured in meters. Dimensions (height, length and width) of all stones sampled in the first month were measured in centimeters and surface area estimated by covering them with metal foil, which was later weighed (Cooper and Testa, 2001). The surface area of subsequent stones was calculated using a regression equation with stone volume as the dependent variable. Land cover characterization was obtained by on-screen digitizing from multi-seasonal, 30 metre resolution Landsat 8 satellite imagery, acquired between April 2013 and June 2014 (Geoterraimage, 2015). The 72 classes land cover data was reclassified into two classes (natural versus non-natural) by means of percentage in the 30x30m resolution image at the quinary catchment level using 1:50 000 mapping and modelling scale.

Statistical analysis

Abundance data were pooled across six stones within a site, as counts of individual stones were zero inflated. Abundance data and its associated predictor variables that were included in the analysis resulted from 14 sites sampled for 12 months, plus an additional 9 sites sampled for 10 months for a total of 258 communities. Co-linearity between environmental variables were explored using Principle Component Analysis (PCA). The first and second principal components explained 30.38% and 18.58% of the total variance respectively. As expected, sites at higher elevations were narrower with colder, slower and more acidic water and smaller rocks (Fig. S3.1). Temperature was negatively correlated with elevation, but temperature was retained in analyses as is biologically more meaningful variable. Similarly, TDS and conductivity were correlated, TDS was retained in the model. We also retained pH which decreased with increasing elevation (Fig S3.1).

Univariate assemblage response was modelled using Generalized Linear Mixed Models (GLMM) in the lme4 package (Nakagawa and Schielzeth 2013; Jamil and ter Braak, 2013). The function ‘glmer’ was used to model species richness based on a Poisson distribution. Sites were included as a random factor to account for temporal pseudoreplication. We included quadratic terms to account for non-linear responses. Model residuals were inspected for normality, heteroscedacity and independence. Models were compared using the Akaike's Information Criterion (Li et al. 2018) to identify those models minimizing the loss of information (Barton, 2018), models with ΔAIC ≤ 2.00 considered equivalent (Burnham and Anderson, 2002).

We fitted multivariate generalized linear models (GLMs) to abundance data of mayfly in the R package “mvabund” (Wang et al., 2012) using the functions “manyglm” and “anova.manyglm”. This model-based approach is superior to a distance-based methods, as multivariate GLMs account for confounding mean-variance relationships that commonly arise in abundance data which contain many zeros (Warton et al., 2012). We used this method to test for an effect of the predictor variables on mayfly assemblages, by summing likelihood ratio statistics for each taxon, yielding a community-level measure for each of the predictors. The log-ratio statistic was calculated for each taxon as a measure of effect for each predictor and summed. Correlation between species was accounted for by using Wald statistics with 999 permutations. This means that the PIT-residual bootstrap method (Warton et al., 2012) was used to derive p-values by resampling 999 rows of the dataset. We first explored the marginal explanatory power of predictors. Then we accounted for temporal autocorrelation by resampling residuals across sampling times within sites, which controls for unaccounted cross-site variation. This was done by specifying site in the block argument of the “anova.manyglm” function (Oksanen et al., 2016). All models, univariate and multivariate, were checked for departure from model assumptions by visually examining plots of residuals against fitted values.

Threshold Indicator Taxa Analysis (TITAN) from the ‘TITAN2’ package (Baker and King, 2010) was used to identify the change-point response of mayfly communities to the predictor variable that explained most of the variation in assemblage structure. The TITAN method uses the standardized z-scores obtained from indicator species analysis (Indicator Value) to detect the taxon-specific change points and the response direction of the taxon along an environmental gradient (Baker and King 2010; Costas et al., 2018). Standardized taxa responses increasing at the change point (z+) are distinguished from those decreasing (z) and those showing no response (Baker and King, 2010). By means of bootstrapping, TITAN estimates indicator reliability and the proportion of times that a taxon is given the same classification in each bootstrap replicate as in the observed data set, as well as uncertainty around the location of individual taxa and community change points (Baker and King, 2010). All statistical analyses were undertaken using R (R Core Team, 2017).

3.3. Results

A total of 11041 mayfly larvae, comprising 19 species in 16 genera and 6 families, were recorded. Species richness varied between 3 and 15 species per site (Table S3.2). *Baetis* and *Dabulamanzia media* were the most abundant genus and species respectively, while *Afroptilum sudafricanum* was the rarest species with only one individual sampled.

The best performing model for predicting mayfly species richness was based on the temperature and pH as parameters ($\Delta AIC \leq 0.4$). Species richness related significantly and negatively to temperature (GLMM: $z = 8.10$, $p < 0.01$), but not pH (GLMM: z = 8.10, p > 0.05) (Fig. 3.2). Fixed effect (R^2_m) explained 4% of the variation in species richness for this model, while fixed and random effects (R^2_c) explained 18%. Based on the AIC, the second best model (AIC = 929.8) included temperature (GLMM: z = -2.681, p > 0.001), pH (GLMM: z = 1.54, p > 0.05) and land cover (GLMM: z = -1.25, p > 0.05). Fixed effect (R^2_m) explained 6% of the variation in species richness for this model, while fixed and random effects (R^2_c) explained 20%. Similarly, temperature and land cover were negatively related species richness and not pH (Fig. 3.2).

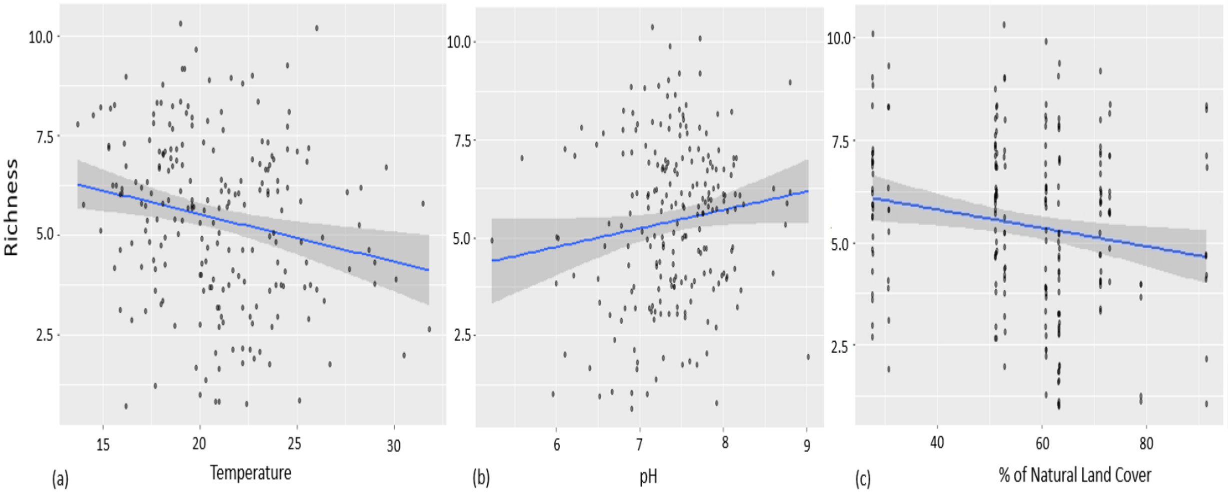

Figure 3.2: Fitted regression for mayfly species richness with increasing (a) temperature (richness declines), (b) pH (richness increases) and (c) percentage of natural land cover (richness declines).

Elevation, temperature, land cover, flow stream, and stone sizes were the most significant variables, explaining most of the variation respectively in species abundance for marginal effects, while conductivity, flow depth and TDS have explained no significant variation (Table 3.1). Including site as a blocking variable (accounting for variation explained by site) also confirms the importance of temperature in structuring assemblages followed by stream flow and stone sizes, while TDS, flow depth, pH, elevation and land cover have explained non-significant amounts of variation (Table 3.1).

Table 3.1: Marginal and Conditional models of the variation in mayfly assemblage structure explained by covariates. Significance:* P < 0.05; ** P < 0.01 and *** P < 0.001.

Covariate	**Marginal Model**	**Conditional model with site as blocking variable**
Conductivity	5.10	35.48 *
Elevation	13.64 ***	2.15×10^{-12}
Flow depth *(m)*	4.46	33.66
Vegetation cover	10.51 ***	2.15 × 10-12
pH	6.67 **	25.85
Stone size (*cm*^{3})	6.86 ***	73.72 ***
Stream Flow	8.47 ***	65.42 ***
TDS *(mg/L)*	4.09	31.50
Temperature *(°C)*	12.58 ***	184.98 ***

Six mayfly species were identified as indicators of change along the temperature gradient (Fig. 3.3). The abundance of five of these taxa declined in response to temperature with threshold temperature of 19 °C (Fig. 3.4). These species were *Nigrobaetis* sp., *Baetis* sp., *Euthraulus elegans, Dabulamanzia media* and *Baetis harrisoni. Nigrobaetis* sp. and *Baetis harrisoni*, all of which were thermophobic. Only one species, *Caenis* sp. had a thermophilic response.

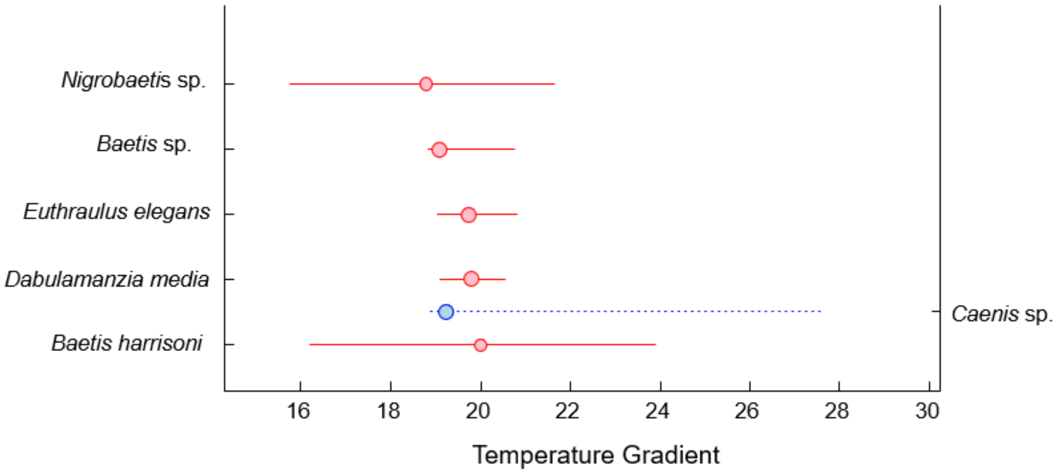

Figure 3.3: Threshold Indicator Taxa Analysis (TITAN) of mayfly species community response to water temperature gradient (°C). Red symbols correspond to negative (z-) mayfly species indicator taxa, and denote taxa that decrease with increasing temperature, and blue correspond to positive (z+) taxa, namely those that increase as temperature increase. Symbols are in size proportional to z scores. Horizontal lines show 5th and 95th percentiles among 500 bootstrap replicates.

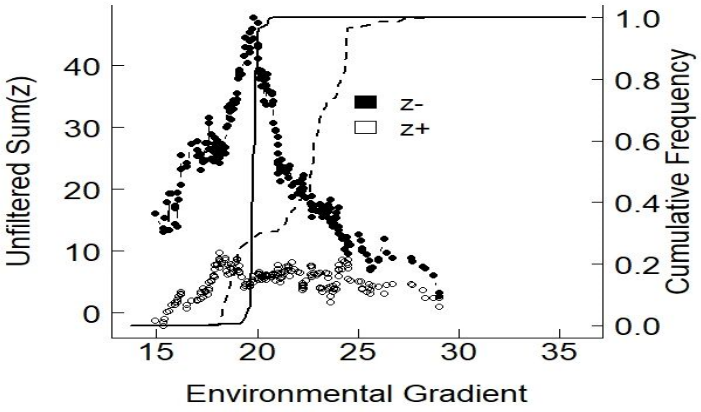

Figure 3.4: Change-point analysis of mayfly species community to temperature. Peaks in sum (z−) and sum (z+) correspond to locations along the gradient where there is synchronous declines (z-) and increases (z+) in mayfly. Solid and dashed lines represent the cumulative frequency distribution of change points among 100 bootstrap replicates for sum (z−) and sum (z+), respectively.

3.4. Discussion

Although mayfly species richness was related to temperature and pH in particular, models explained a very small amount (i.e. 4%) of richness variation. Site specific characteristics not measured explained considerably more but still not a large amount of variation. Covariates included in univariate models also featured in multivariate models. Temperature in particular consistently explained significant amounts of variation and analysis of threshold responses of the mayfly community to temperature suggest that 85% of indicator species in the Luvuvhu catchment are thermophobic, decreasing with increases in temperature.

Gustafson (2008) provided evidence for the importance of temperature in structuring mayfly communities. Though literature on life histories patterns of Afrotropical mayfly diversity are scarce (Barber-James et al. 2008), evolutionary history suggests that the emergence of many mayfly species has always depended on temperature for their organismic, population, and species levels of organization (Edmunds, 1972; Wolda and Flowers, 1984; Brittain, 2008). A number of studies have indicated water temperature as the most important environmental driver of assemblage structure of mayfly community (Gustafson 2008; Haidekker and Hering 2008; Vilenica et al., 2017b). This is because temperature is closely related to species traits such as embryonic development, nymphal growth, emergence, metabolism and survivorship of many taxa (Haidekker and Hering 2008; Dallas and Rivers-Moore, 2012; Vilenica, Ivković, et al. 2017; Dallas and Rivers-Moore, 2018).

The level of pH also played a considerable role in explaining mayfly assemblage structure. This water parameter regulates important physiological functions of mayflies, including the exchange of ions with the water and respiration (Svitok 2006; Kubendran et al., 2017; Vilenica et al, 2017a) which otherwise is impossible to operate normally under extreme pH values (>8.5 and < 6.5) (Klonowska-Olejnik and Skalski 2014). In this study, water tends to get more acidic at higher elevations, while there were more human activities taking place (such as sewage discharge, car washing, body and clothes washing, animal grazing and subsistence farming) at lower elevations. According to

Kubendran et al. (2017), increasing pH are caused by detergents and bathing soaps which have also been a concern in large areas of the Luvuvhu catchment (Kleynhans, 1996; Traoré et al., 2016).

Stream flow was another important environmental driver of mayfly species abundance or occurrence. A study by Klonowska-Olejnik and Skalski (2014) showed that reduced populations of mayfly communities was linked to frequent flooding and increased discharge due to heavy rainfall. This is not surprising given the influence of stream flow as a result of stream regulation which causes numerous changes (Bunn & Arthington 2002), affecting complex hydraulic variables (velocity, depth, substrate roughness) impacting mayfly assemblage structures (Brooks et al. 2005; Klonowska-Olejnik and Skalski 2014; Salmaso et al., 2018). With increasing stream flow variability and declining stream flow volumes in the Luvuvhu catchment due to increasing water abstraction and climate variability (Kleyhans, 1996; MacFadyen et al., 2018; Ramulifho in review), this may decrease abundance or diversity of mayfly as well their ecosystem productivity (Boyero et al., 2011).

In a tropical region of south-eastern Brazil, Siegloch *et al.* (2014) showed a 57% reduction in mayfly richness in streams with decreased natural vegetation cover. Pond (2010) also found that mean mayfly richness and relative abundance were significantly higher in naturally vegetated catchments. The high natural vegetation cover percentage of this study occurred at the lower parts of Luvuvhu catchment, but this region is characterized by high human activities (subsistence agricultural and settlement activities) and flow modification as also noted by Kleynhans (1996) (Fig. S3.2). The replacement of natural vegetation with alien plants in the upstream parts of the Luvuvhu catchment is associated with both large scale commercial timber production and macadamia orchards. However, riparian zones in the upstream parts of the Luvuvhu catchments are largely intact and have retained high density of riparian canopy as compared to the lower catchment (high natural vegetation cover percentage), explaining high abundance in this section. Remote sensing classification of vegetation cover neglected riparian corridors of natural vegetation where riparian vegetation maintained and no real water extraction in these forests. This strongly contrasts with the high natural vegetation cover percentage where riparian vegetation along the stream banks is actively being removed. Riparian vegetation cover has great impact on temperature and nutrient levels in a stream which consequently determines the integrity and species distribution in river system (Orwa et al., 2013).

Mayfly species are mainly shredders and grazers and their abundance and distribution are also closely associated with riparian vegetation cover (Siegloch et al., 2014; Sartori and Brittain, 2015; Barber-James, 2016). As shredders, the distribution and occurrence of mayfly species as influenced by riparian conditions and leaf litter characteristics is linked to the availability of food and shelter (Boyero et al., 2011), because they process large amounts of organic matter originating from riparian vegetation (Moulton et al., 2004), while also forming an important prey for fish (Sartori and Brittain, 2015). The reduction of mayfly due to clearance or removal of forest results in altering of primary production (nutrient cycling) and system dynamics, due to the input of fertilizers and pesticides from agricultural activities (Siegloch et al., 2014). This is also the same in the temperate regions (northern hemisphere) where different set of environmental conditions are experienced, but species declines with declining canopy (Svitok, 2006; Klonowska-Olejnik and Skalski, 2014; Vilenica et al., 2017b).

Identifying reliable indicator taxa and their responses to changing environmental gradients is of major concern for the development of management tools for freshwater ecosystems (Costas et al. 2018). In this study, the majority of mayfly species (83 %) responded negatively to increased water temperatures, while 17 % of mayfly increased with increasing water temperature. Similarly, a study by Rivers-Moore et al. (2012) associated rising temperature to loss of thermal habitat conditions for cold-adapted mayflies. A study by Chessman (2012) found that as one of most thermally vulnerable and thermorphobic species, the majority of mayfly species in affected regions will need to extend their distribution to suitable and accessible habitats at higher altitudes (e.g. Walther, 2010; Bush et al., 2012; Filipe et al., 2012). Laboratory assays of *L. penicillata*, a mayfly species of conservation importance, also found that the chronic thermal stress threshold, ranged from 19.2 between 20.7 °C depending on season (Dallas and Rivers-Moore, 2018). This coincides with our field-based observation of 19 °C and provides compelling support for the importance of these temperatures to both individuals and community level responses. A field-based observation by Vilenica et al. (2017a) also identified threshold responses at 18 °C for some mayfly species inhabiting the mountainous rivers in the Mediterranean region. In general, mayfly species are thermally sensitive species and findings from the current study seem to point largely to the existence of their critical inflection point between 18 to 20 °C (Vilenica et al., 2017a; Dallas and Rivers-Moore, 2018).

Changes in mayfly assemblage structure could therefore directly affect ecosystem processes such as nutrient cycling, algal distribution, retention and distribution of organic matter, and predator-prey interactions (Wallace and Webster, 1996; Liess and Hillebrand, 2004; Sartori and Brittain, 2015). Boyero et al., (2011) indicated that quantifying the importance of this energy dynamics and establishing clear causal predator-prey relationships patterns remains an important challenge, given the complexity of interactions between environmental constraints and the quality and availability of resources. However, available evidence shows that mayfly species are generally primary prey for invertebrate predators (Wallace and Webster, 1996).

The significant impacts of climate change and instream impoundments on hydrologic regimes will undoubtedly lead to significant changes in mayfly communities (Brittain, 2008; Rivers-Moore et al., 2012; Sartori and Brittain, 2015). However, warming of stream water due to the effects of global warming can be reduced by maintaining instream habitat and riparian zones; and limiting hydrological abstraction to increase resilience in freshwater ecosystem (Dallas and Rivers-Moore, 2018). We have provided evidence for the importance of thermal regimes in structuring mayfly assemblages with real implications for mayfly diversity under global change scenarios that include climate and land use. Since the presence or absence of certain mayflies is strongly influenced by temperature, as indicators, mayflies can help to establish levels of thermal degradation or the recovery in freshwater ecosystems.

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Chapter 4: Streamflow as the main determinant of blackfly diversity in the Luvuvhu catchment

Abstract

Blackflies are amongst the most abundant and diverse group of aquatic insects and are rarely absent from rivers and streams, with distributions of these species largely driven by current velocity, conductivity and turbidity. Research on blackflies has mainly focused on medical, veterinary and economic importance, while community ecological studies in the Afrotropical Region are scarce. The aim of this study was to determine the response of blackfly species to environmental drivers in the north-eastern tropical regions of South Africa. A total of 1343 larvae, representing seven blackfly species in four subgenera were collected from 23 sites. Water temperature and flow were the most significant drivers of richness, while conductivity, land cover and flow had the strongest effect on blackfly species abundance across species and sites. Threshold Indicator Taxa Analysis (TITAN) identified no indicator taxa and multiple change points for both conductivity and land cover gradient change. TITAN demonstrated that blackfly communities do not respond in a synchronous manner along an environmental gradient. Information on flow, conductivity, landcover and other environmental factors preserving aquatic life is essential to the development of conservation and management programs for rivers and their related ecosystem services in South Africa.

Keywords

Blackfly, Limpopo province, multivariate analysis, streamflow, TITAN, water temperature.

4.1. Introduction

Globally, blackflies constitute amongst the most abundant and diverse group of aquatic insects with 2142 extant species that occur ubiquitously across most lotic systems (Landeiro et al., 2009; Adler and Crosskey, 2019). Blackflies (Diptera: Simuliidae) are also common aquatic taxa in tropical regions of the world (de Moor, 1999; Figueiró et al., 2012), with more than 211 species from the Afrotropical Region alone (de Moor, 2017). Despite such diversity, this group shares broad life history attributes. Larvae and pupae generally attach themselves to various submerged objects (such as fallen leaves, rock surfaces, trailing grasses, tree roots and mud) in many types of lotic environments, ranging from large rivers to tiny spring-fed trickles, and from swift currents to water that barely moves (Srisuka et al., 2015). Blackfly larvae are important components of lotic ecosystems as filter-feeders, and are often present in very high densities, reaching up to one million larvae per m^2 in some rivers (Malmqvist et al., 1999; Couceiro et al., 2014). These filter feeders are among the insects best adapted to life in swift-flowing water and the absence of running water is, in most cases, a limiting factor preventing the abundance of blackfly larvae and pupae (Bandason et al., 2014; de Moor, 2017) and are largely limited to riffles, rapids, and cascades (Rivers-Moore and Palmer, 2018).

Variation in environmental factors contributes to spatial and temporal partitioning of species composition at local (alpha diversity) and regional (beta diversity) scale (Zhang et al., 1998; Landeiro et al., 2009). The micro-distribution (spatial = site or reach or areas < $10m^2$; temporal = daily) is largely explained by biotic factors such as trophic relationships and food availability (Rivers-Moore et al., 2006; Figueiró et al., 2012), while meso- and macro-distribution (spatial = regional or areas > 10 m^2 to kms; temporal = days (seasonal) to years) of blackfly larvae is largely driven by abiotic factors such as water current velocity, conductivity and turbidity (Rivers-Moore et al., 2006; Başören and Kazanci, 2011; Bandason et al., 2014; Rivers-Moore and Hill, 2018).

Blackfly are useful ecological health indicators for a number of reasons. On the one hand, different blackfly species have different labral fan structures, which determine competitive abilities in feeding efficiencies in response to different stream flow velocities (Palmer and Craig, 2000). Given this relationship, the occurrence of different species and their relative abundances can be used to understand changes in flow volumes within a catchment over time (Palmer and Craig, 2000; Feld et al., 2002). On the other hand, the life cycle strategies (e.g. growth rates) and duration of the aquatic stages of blackfly (the developmental time from egg through various larval instars to pupal stage and the adult emergence) can be used to understand water temperature regimes (Rivers-Moore et al., 2006; Reidelbach and Heino, 2002). Blackfly larvae have relatively shorter life cycles (from egg to adult can be completed in less than 2 weeks) than those of many other macroinvertebrate groups and this decreases the duration in which blackfly larvae are at risk of mortality induced by flow disturbance or predation (Zhang et al., 1998). Several factors have been proposed to explain survival and dominance of blackfly species. Generally, models have shown that survival and dominance are sensitive to water velocity, turbulence, particle concentration, and filter structure (Palmer and Craig, 2000).

Because of the group’s widespread occurrence and abundance, habitation in various types of running water and sensitivity to different environmental change, blackfly are an important taxonomic group for indicating anthropogenic activities in rivers (Feld et al., 2002; Beyene et al., 2009; Mereta et al., 2012; Ambelu et al., 2014; Couceiro et al., 2014). The occurance of blackfly community also reflect primary production and the ability of aquatic systems to support vertebrate wildlife (e.g. fish) and remove pollutants (particles) through their filter feeding mechanisms (Feld et al., 2002; Mereta et al., 2012). Metrics of blackfly species (e.g. richness composition, tolerance levels) and life cycle strategies (e.g. feeding strategies) can be used to inform decision making, while monitoring of such metrics will show management effectiveness (Ambelu et al., 2014).

There are numerous reports of blackfly epidemics in South Africa, including their biting nuisance, transmission of pathogens that affect human health and even livestock (Myburgh and Nevill, 2003; Rivers et al., 2003; 2018). However, ecological studies on the blackfly fauna of the Afrotropical Region are scarce compared to studies from other regions of the world (Cheke et al., 2017) and studies on blackfly medical, veterinary and economic importance in South Africa (Myburgh and Nevill, 2003). In South Africa, most of the available literature is focused on the Orange and Great Fish Rivers because of the periodic outbreaks of pest blackfly species (e.g. *Simulium chutteri*) linked to changes in stream flow regime due to construction of impoundments (O'Keeffe and de Moor, 1988; Rivers-Moore et al., 2008; Rivers-Moore and Palmer, 2018), as compared to rivers in the northern region of the country. One important catchment in these semi-arid region of the country in terms of freshwater biodiversity (Evans, 2017), the Luvuvhu River catchment, has experienced declines in terms of streamflow volume over a 86-year period (Ramulifho et al., in review). Blackfly diversity has received almost no attention in this catchment and it is unknown if changes in environmental factors in the blackfly larvae habitats could lead to pest outbreaks of blackfly populations.

Given that patterns of species distribution and abundance can provide insight into the mechanisms that structure species assemblages, the aim of this study was to determine the response of blackfly species to local and regional factors. To achieve this, we identified three objectives; (i) to describe blackfly species community composition, (ii) evaluate the role of environmental variables as drivers of blackfly abundance and richness in riffle biotopes, and (iii) detect change-point responses of blackfly species (indicator taxa) along most influential environmental gradients. Because the larvae of blackfly species show specific preferences for environmental conditions, results from this study can be used to predict species distribution and guide restoration efforts of streams and rivers.

4.2. Methods

Study area

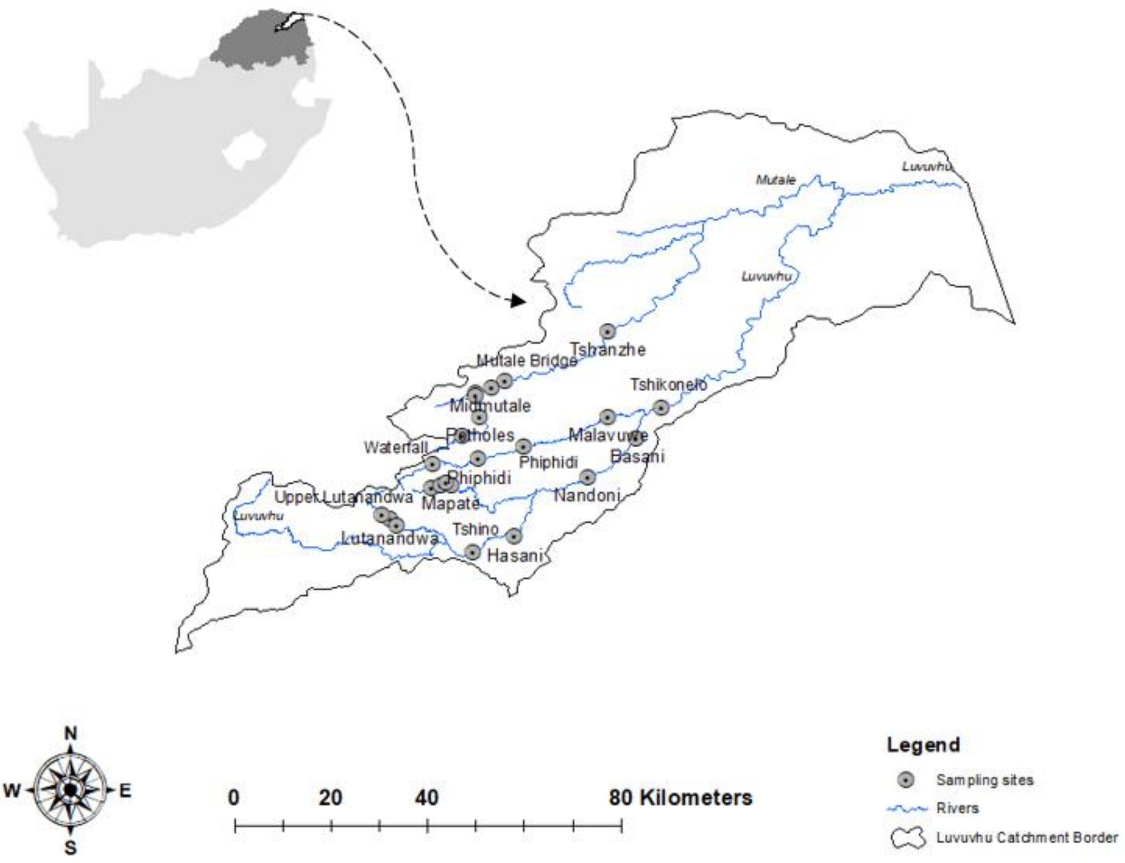

Figure 4.1: Map of the Luvuvhu catchment, South Africa with the position of blackfly sampling sites. Insert shows location of the study area within Limpopo province and South Africa.

We studied the tributaries of the Luvuvhu catchment that originate on the eastern escarpment of the Soutpansberg Mountains, a recognized southern African center of endemism (Joseph et al. 2019) in a strategic water source area in South Africa (Nel at al., 2013). This catchment of about 5 940 km^2 is located between the geographical coordinates of 30° 7'43.95" to 31°23'14.92" E and 22°29'17.50" to 23° 7'5.40" S (Fig. 4.1). The mountainous areas to the west of this catchment receive the highest mean annual precipitation (MAP) of 1 800 mm, compared to a MAP of 440 mm in the lowland areas which include the Kruger National Park (Kleynhans, 1996). However, the MAP of the entire catchment varies from 610-800 mm (DWA, 2012). The mean annual runoff (MAR) is 519 million m^3 and altitude ranges from 232 to 1587 masl (DWA, 2012). While rainfall has remained largely the same over the past 100 years in some areas of the Luvuvhu catchment (MacFadyen et al., 2018; Nkuna and Odiyo, 2016), stream flow variability has increased with decreasing flow volumes in the Luvuvhu River Catchment over an 86-year period, linked to anthropogenic activities such as commercial agriculture and abstraction (Ramulifho et al., In review).

Blackfly sampling

We sampled blackflies at 23 sites across six perennial rivers of the Luvuvhu catchment (Fig. 4.1; Table S4.1). Fourteen sites were sampled monthly over a one year period, between December 2016 and February 2018 and an additional nine sites were added to the 14 sites to increase representation of the environmental gradient, limiting the influence of extreme observations. Sampling was limited to the stones-in-current biotope, with selection of substrate focusing on cobbles of 10-25cm in size. During sampling at each site, six stones were rinsed and brushed with a toothbrush to dislodge organisms. Organisms were collected in a net (30 × 30 cm diameter; 250 μm mesh) placed immediately downstream of each of the six stones. Contents of the net were emptied into a sample holding bottle with 70% ethanol and sorted to their lowest taxonomic level in the laboratory. Specimen collection was identified to the subgenera or species group using Day et al. (2002), and confirmed by taxonomic specialists at the Albany Museum, South Africa. Reference specimens of blackflies from this study were deposited at the Benthic Macroinvertebrates collection of the SARChI Chair on Biodiversity value & change in the Vhembe Biosphere Reserve, University of Venda, South Africa.

Environmental variables

At each site, we collected instantaneous measurements of water physico-chemical parameters (water temperature, pH, total dissolved solids (TDS), and electrical conductivity (EC)) using handheld Crison pH/mV meters. These variables were collected during mid to late afternoon, when rivers exhibit maximum diel water temperature (Dallas et al., 2012).We measured stream flow and flow depth using a flow meter FP101 (Global Water), while river width and elevation were measured using handheld GPS device. The dimensions (height, length and width) of all stones sampled were measured to quantify colonisable surface area and calculate blackfly densities. The surface area of subsequent stones was determined using stones sampled in the first month, by covering them with a metal foil, which was later weighed (Cooper and Testa, 2001) and regressed using foil weight as an independent variable and surface area as the dependent variable. Land cover characterization was obtained from remotely sensed data reclassified into two classes (natural versus non-natural) at a scale of 1:50 000 (Geoterraimage, 2015).

Statistical analysis

We ran all statistical analyses using R statistical software (R Core Team, 2019). We determined the relationship between all environmental variables measured during sampling together with land cover data using Pearson product-moment correlation, which draw a line of best fit through the data of two variables. Non-correlated variables that are ecologically relevant were used in blackfly diversity modelling. Data from the six stones were pooled into one sample as finer scale data was zero-inflated and models did not converge.

To model relative strength of species richness responses, we used Generalized Linear Mixed Models (GLMM) from the 'lme4' package (Nakagawa and Schielzeth 2013; Jamil and ter Braak, 2013). The function 'glmer.nb' with a log-link function was used to model species richness. During the analyses, sites were used as a random factor to account for temporal pseudo-replication. Akaike's Information Criterion (AICs) was used to compare models, where the lowest AIC value represents the best model (Li et al. 2018). Marginal R^2 (variation explained by fixed effects only) and conditional R^2 (variation explained by fixed and random effects) were calculated for the best and second best model (Nakagawa and Schielzeth, 2013).

The relationship of blackfly community composition to predictors was modelled using Permutational Multivariate Analysis of Variance (PERMANOVA). This multivariate approach was run using the 'adonis' function in the vegan package in R (Jari et al., 2019). PERMANOVA is a geometric partitioning of multivariate variation in the space of a chosen dissimilarity measure according to an ANOVA design, with p-values obtained using appropriate distribution-free permutation techniques (Anderson, 2017). The PERMANOVA method partitions the variance across one or more explanatory factors, allowing simultaneous testing for the effect of multiple factors (Loomer et al., 2019). Testing was performed with 999 permutations using Euclidean distance as the resemblance measure and Type II sums of squares with fixed effects set to sum to zero (Jari et al., 2019).

Threshold Indicator Taxa Analysis (TITAN) in 'TITAN2' package in R (Baker et al., 2015) was used to identify change-point response and indicator taxa of blackfly communities to the most important predictor. Change-point analysis is a non-parametric technique that orders and partitions observations along an environmental gradient (Baker and King 2010). Using the standardized taxa responses, we analyzed the blackfly taxa dataset and compared the change-point response of blackfly to the most important environmental variables as determined by the multivariate model. TITAN uses Bootstrapping to estimate indicator reliability and purity as well as uncertainty around the location of individual taxa and community change points. (Baker and King 2010; Joseph et al. 2019). TITAN shows standardized taxa responses increasing at the change point (z+) distinguished from those decreasing (z) and those showing no response (Baker and King 2010).

4.3. Results

The Spearman's rank correlation coefficient results (Fig. 4.2) indicated that TDS and conductivity were statistically highly positively correlated ($R^2 = 0.95$), and TDS was retained for blackfly response modeling. The highest negative statistical correlation was between temperature and elevation ($R^2 = -0.77$) with temperature retained in subsequent models. Variables that were uncorrelated included land cover with width, and pH with flow flow. In general, results indicated that sites at higher elevations were typically narrower, shallower, colder, faster flowing, and more acidic with smaller rock volumes (Fig. 4.2).

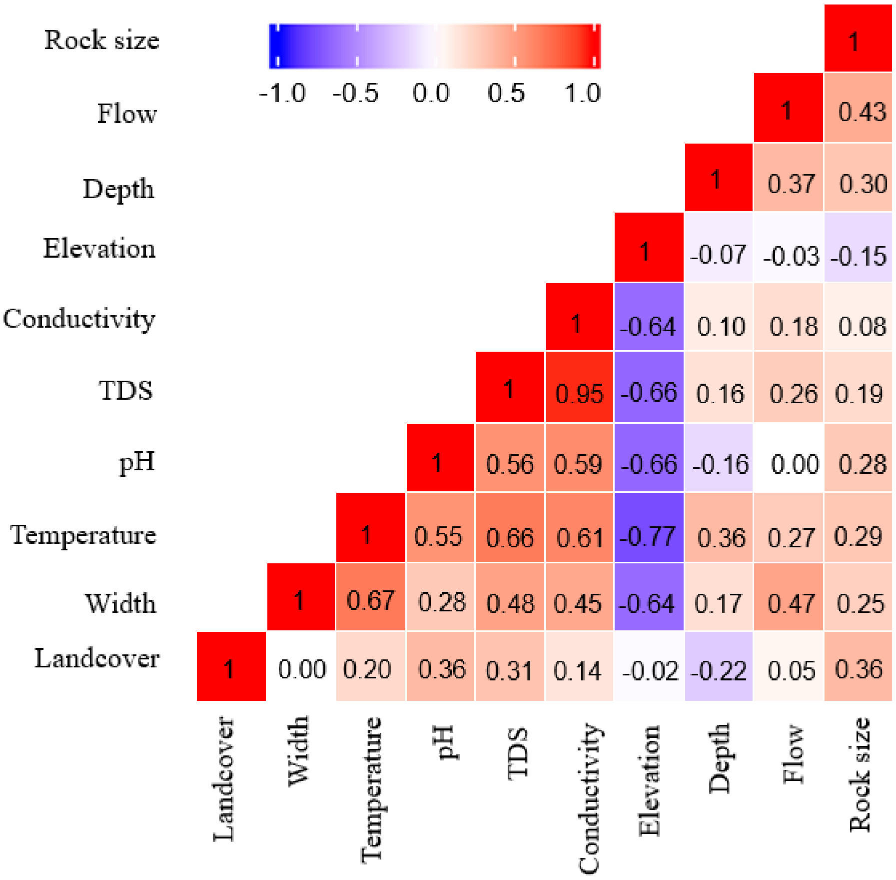

Figure 4.2: Spearman's rank correlation coefficient between environmental variables. Correlation coefficients are colored according to the value of association between ≤ 1 and ≥ -1.

Community composition

A total of 1343 larvae, representing seven blackfly species from four subgenera (namely; *Simulium (Edwardsellum*), *Simulium (Meilloniellum*), *Simulium (Metomphalus*), and *Simulium (Pomeroyellum)*) were collected from 23 stream sites across Luvuvhu catchment (Table S4.2). Only one site (Tshanzhe) recorded no blackflies. In cases where cryptic species were encountered, their species complex name is referred to. For example *S.(M.) hargreavesi* and *S.(M.) chutteri* were referred to as *Simulium (Metomphalus) hargreavesi/chutteri*. In the case of this study, these species were under developed (tiny) to correctly identify them and pupae (rear identification) were not found at any our sites. Those that we identified, at the species level, the medusaeforme species group belonging to the *Simulium (Metomphalus)* was the most diverse with three species (*S.(M.) vorax*, *S.(M.)*

medusaeforme, *S.(M.) hargreavesi/chutteri*). *Simulium (Meilloniellum)* subgenus had two species (*S.(M.) adersi* and *S.(M.) hirsutum*), while *Simulium (Edwardsellum)* and *Simulium (Pomeroyellum)* also had one species each (*S.(E.) damnosum s.l* and *S.(P.) sp*. (unknown species)) respectively. *S.(M.) hargreavesi/chutteri* was the most abundant species followed by *S.(M.) vorax*, while *S.(M.) hirsutum* was the rarest species (Table 4.1). *S.(M.) hargreavesi/chutteri*, *S.(M.) adersi*, and *Simulium (pomeroyellum*) was the most widespread (20/23 sites or 86.95%).

Table 4.1: Total numbers of site occurrence and abundance for each blackfly species.

Species name	**Species occurrence frequency**	**% of species occurrence**	**Species abundance**	**% of species abundance**
S.(E.) damnosum s.l.	16/23	70	153	11.39
S.(M.) adersi	20/23	87	167	12.43
S.(M.) hargreavesi/chutteri	20/23	87	300	22.34
S.(M.) hirsutum	07/23	30	71	5.29
S.(M.) medusaeforme	17/23	74	221	16.46
S.(M.) vorax	15/23	65	240	17.87
Simulium pomeroyellum	20/23	87	191	14.22

Blackfly species richness

The best model for blackfly species richness had an AIC value of 681.3 and included temperature, flow and TDS. Of these variables, temperature and flow were the most significant drivers, with richness declining with increasing temperature (GLMM: estimate = -0.35, $p < 0.001$) and increasing with flow (GLMM: estimate = 0.55, $p < 0.001$) (Fig. 4.3). R^2_C explained 25 % variation as compared to 16% of the R^2_m. The second best model had the AIC weight of 682.5 and includes temperature (GLMM: estimate = -0.35, $p < 0.001$), flow (GLMM: estimate = 0.57, $p < 0.001$) and land cover (GLMM: estimate = 0.10, $p > 0.05$). Blackfly species richness was therefore positively related to percentage of natural land cover. In the second best model, R^2_c explained 2% less variation as compared to the best model, while R^2_m remained the same as in the best model.

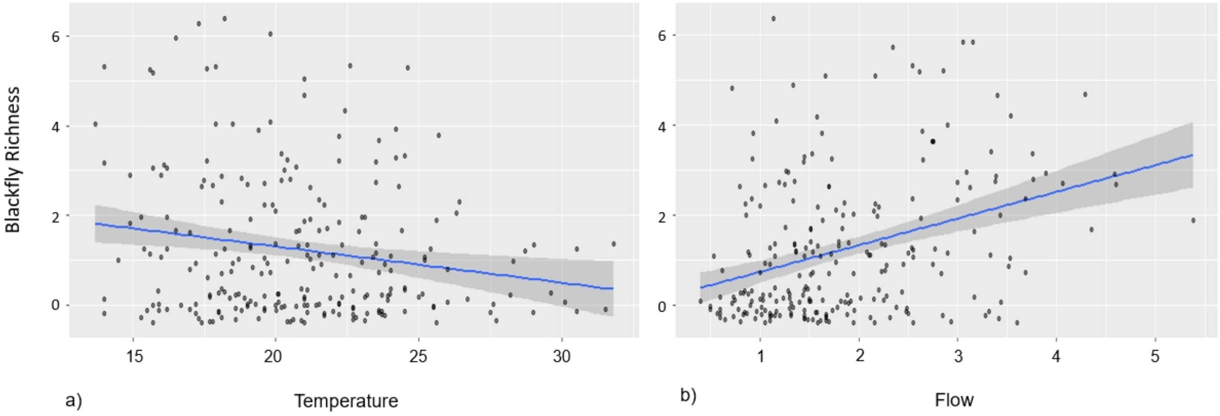

Figure 4.3: Fitted regression between species richness, (a) temperature and (b) flow from the best model.

Assemblage structure

Conductivity and land cover had the strongest influence on blackfly assemblage structure across species and sites based on the high R^2 and explained significant amounts of variation (Table 4.2). Flow had explained stronger amount of variation with a relatively higher R^2, but it was not significant. The weakest amount of variation was explained by stream flow depth and stream width which all had the lowest R^2 of 0.02 (Table 4.2)

Table 4.2: PERMANOVA analysis of environmental variables' effects on blackfly assemblage structure based on the Bray–Curtis dissimilarities. Significant variables are indicated by * P < 0.05; ** P < 0.01 and *** P < 0.001.

Environmental variables	**F.Model**	**R^2**	***p value***
Conductivity	2.16	0.09	0.04*
Land cover	2.16	0.09	0.03*
Temperature	1.13	0.05	0.35
Elevation	1.00	0.04	0.45
Depth	0.46	0.02	0.87
Width	0.41	0.02	0.92
Flow	1.90	0.08	0.06
Rock size	0.62	0.03	0.77
TDS	0.72	0.03	0.66
pH	0.62	0.03	0.75

Threshold indicator analysis

TITAN identified no indicator taxa for both conductivity and land cover gradient (Table S4.3). Because of this, it was also not possible to establish a definite change point for the blackfly community for these two explanatory variables (Fig. S4.1 and S4.2). However, we found evidence of multiple change points which are pronounced between the value of 20 and 23 µS/cm for conductivity and between 50 and 70% of natural vegetation land cover gradient (Fig. S4.1 and S4.2). A contrasting response has been observed for blackfly species along the stream flow gradient. TITAN identified *S.(M.) hargreavesi/chutteri* as an indicator taxa had a positive (z+) threshold response (increased) at 1.6 m/s (Fig. 4.4).

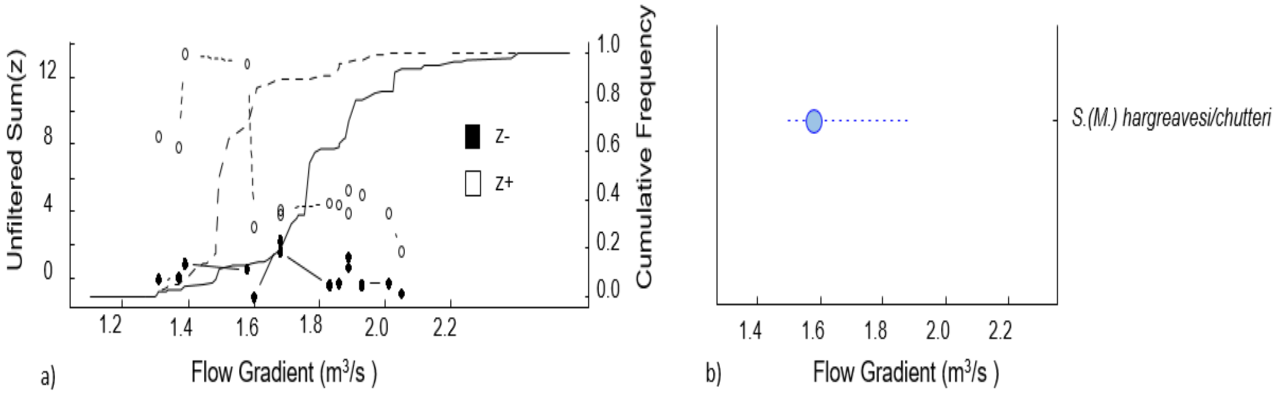

Figure 4.4: TITAN (a) sum (z-) and sum (z+) values for all possible change points of blackfly community in response to flow gradient and (b) change-point analysis (Bray-Curtis distance) of blackfly community response (purity≥ 0.95, reliability ≥ 0.95, $P < 0.05$) to a stream flow gradient. Dotted lines represent the 95th quantile intervals for each change point, while filled symbols (●) correspond to sensitive taxa (z−).

4.4. Discussion

Drivers of blackfly richness and assemblage structure

The findings in this study are consistent with studies from around the world which have also reported that blackfly richness decreases with increasing temperature while increasing with flow (e.g. Hamada et al 2002; Yacob et al., 2016; Cheke et al., 2017). In South Africa, studies have shown the importance of stream flow as one of major driver of blackfly local richness (Rivers-Moore et al., 2006; Rivers-Moore et al., 2007; Rivers-Moore and de Moor, 2008). For example, low and warmer flow conditions create unfavorable habitats for the development of large populations of most blackfly species such as *S. chutteri* (Rivers-Moore et al. 2007). Several surveys along the Orange and Vaal Rivers have also attributed high abundance and richness of blackflies in the 1980s and 90s, and outbreaks in 2000 and 2001, to higher-than-normal stream flow levels (De Beer and Kappmeier Green, 2012) and more favorable water temperatures (Rivers-Moore et al., 2007). However, there is no record of pest blackfly outbreaks in the Luvuvhu catchment, and it is unknown if this relates to the declining stream flow volume as reported by Kleynhans (1996) and Ramulifho et al., (2019). Published blackfly outbreak models indicate that flow reduction in flow effectively reduces the likelihood of blackfly outbreaks (Rivers-Moore et al., 2008; Ambelu et al., 2014).

Srisuka et al. (2015) demonstrated that riparian vegetation is one of the most important factors affecting blackfly communities. Riparian and in-stream vegetation create additional breeding surfaces for blackfly (Myburgh and Nevill, 2003), habitat to attach for food acquisition (Malmqvist et al., 1999), shelter against water current and predation (Mereta et al., 2012), a place for oviposition and fixing pupal cocoons. (Feld et al., 2002) and habitat enrichment (Srisuka et al., 2015). High densities of blackfly species are associated with riparian vegetation because they provide attachment stands than do bare sand or gravel, since blackfly larvae need firm contact with the substratum for difference functions (Feld et al., 2002). A study by Kazanci (2006) indicated that some blackfly species cannot tolerate loss of riparian vegetation caused by climate change as this riparian vegetation provides irreplaceable services, such as food and shelter. As also indicated by Srisuka et al. (2015), the results of this study also demonstrated that vegetation is one of the most important factors influencing species assemblage. Therefore, vegetation is known to be an important factor influencing blackfly communities.

Our measured conductivity values in this study were generally low, ranging between 2.34 and 86.10 μS/cm, which is well within the tolerance range of some of *Simuliium* species such as S. *chutteri* (Rivers-Moore and Hill, 2018). Several other studies have also indicated that the abundance of blackfly changes in response to conductivity (Couceiro et al., 2014; Srisuka et al., 2015). Feld et al. (2002) recorded no blackfly species at heavily modified sections where conductivity reached high level of 1740 μS/cm. A study by Mereta et al., (2012) found that the abundance of blackfly decreased with increasing conductivity in dry season. Bandason et al. (2014) found that blackfly larvae densities were positively related to flood-induced increases in conductivity. The results of the current study also show that conductivity is an important variable in determining the presence or absence of blackfly species. In contrast, findings by Rivers-Moore and Hill (2018) recorded a little relationship between blackfly species abundances and high conductivity levels in the Orange River of South Africa. High level of conductivity is often associated with urbanization and high surface runoff from agricultural lands, with high flow rivers likely to reflect dilution effects (lowering conductivity level) by runoff and precipitation (Roy et al., 2003; Edokpayi et al., 2005).

A recent study by Rivers-Moore and Palmer (2018) in the Orange River reported that blackfly species assemblage structure was also largely governed by another physio-chemical parameter, turbidity. Edokpayi et al. (2005) found significant difference ($p < 0.006$) in the level of turbidity between the wet and the dry seasons in some rivers of the LRC. This shows that the Luvuvhu catchment system does alternate between turbid and clear running water, just like in the Orange River of South Africa (Rivers-Moore and Palmer, 2018). Unfortunately, turbidity level was not measured in this study and thus limited the empirical evaluation of its significance to blackfly assemblage. However, the results from Rivers-Moore and Palmer (2018) and Rivers-Moore and Hill (2018) indicated that changes in turbidity caused switches in blackfly species composition and abundance, with *S. chutteri* unlikely to occur at large densities at clear running water (de Moor, 1994; Rivers-Moore et al., 2007).

Threshold Indicator Taxa Analysis (TITAN)

TITAN identified one indicator species of blackfly community change (*S.(M.) hargreavesi/chutteri*), but several studies have suggested different threshold points for this species in the flow gradient as opposed to 1.6 m/s of this study (Fig. 4.4). A study by Rivers-Moore et al. (2008) showed a threshold of 2 m/s for *S. chutteri*. Another study by Rivers-Moore et al. (2007) reported that a velocity threshold of 1 m/s exists for *S. chutteri*. Since *S.(M.) hargreavesi/chutteri* was also a frequent and dominant species, our TITAN results also confirms that *S. chutteri* is likely to occur in large densities at flow velocities of more than 1 m/s as reported by Rivers-Moore et al (2006). This species is one of the most important pest species (De Beer and Kappmeier Green, 2012), and as a result of an increase in high-velocity biotopes, *S. chutteri* populations is prone to outbreaks and outnumbering other invertebrate species (Rivers-Moore et al., 2008).

For other major drivers of blackfly assemblage in this study (land cover and conductivity), TITAN could not identify any indicator species nor definite change point thresholds, but it allowed us to determine multiple synchronous change points for these gradients. This confirms that blackflies respond at different points of the gradient and are comparatively insensitive to environmental changes (Rivers-Moore and Palmer, 2018). The multiple change points could be due to a limited abundance of reliable indicator taxa and as these exhibit broad ineffectual confidence intervals (Costas et al., 2018). According to Baker & King (2010) a single reliable community threshold is based on synchronous changes in the abundance of many indicator taxa within a narrow range of the considered predictor gradient. The multiple thresholds of blackfly community provides evidence that most species display varying degrees of generalized life history patterns with several period of feeding and laying of eggs per annum and similar potential fecundities, making these species able to thrive not only on varying conductivity but also on regulated conditions (Rivers-Moore and Palmer, 2018).

4.5. Conclusion

Our study provided fundamental information on assemblage structure of blackflies species in Luvuvhu catchment. Water temperature, stream flow, conductivity, and landcover, respectively, showed a significant effect on the distribution of blackfly species. Stream flow and water temperature dominated as drivers of species richness, while species abundance was largely driven by conductivity, vegetation cover and flow. The new information obtained from this study provides an insight that emphasizes on the importance of protecting and managing the natural water temperature and stream flow, which are currently securing high diversity of blackfly species. As water temperature and stream flow changes due to global change (Davis and Vincent, 2017), the assemblage structures of blackfly species in this region is likely to change.

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Chapter 5: Challenges to Implementing an Environmental Flow Regime in the Luvuvhu River Catchment, South Africa

Abstract

Rivers are now facing increasing pressure and demand to provide water directly for drinking, farming and supporting industries as a result of rapidly growing global human population. Globally, the most common practice for catchment managers is to limit water abstraction and changes to stream flow by setting environmental flow standards that guard and maintain the natural ecosystem characteristics. Since the development of the environmental flow concept and methods in South Africa, very few studies have assessed the institutional constraints towards environmental flow implementation. This study determined stream flow trends over time by fitting simple linear regression model to mean daily stream flow data at three selected stations in the Luvuvhu River Catchment (LRC). We also conducted a literature search to review, firstly the response of aquatic organisms (fish and macroinvertebrates) to changes in habitat conditions; and secondly on local challenges affecting the sustainable implementation of environmental flow regime and related water resources management strategies. All three stream flow stations show decreasing stream flow volumes, faster in some stations with the possibility that flow will cease in the near future. Qualitative analyses from both local and international literature searches found that the main challenges facing the implementation of sustainable flow strategies and management are absence of catchment management agency, lack of understanding of environmental flow benefits, limited financial budget, lack of capacity and conflict of interest. Rivers with changing stream flows tend to lose sensitive species. The development of scientifically credible catchment-wide environmental flow and abstraction thresholds for rivers within the LRC would make a major contribution in minimizing the declining stream flow volumes. Monitoring and reporting should be prioritized to give regular accounts of the state of our rivers.

Keywords: Catchment management; Environmental flows; Luvuvhu Rivers; Stream flow; Water allocation; Water use.

5.1. Introduction

River scientists are challenged by the question of how much water a river needs to maintain its natural health and to sustain the integrity of aquatic and riparian ecosystems. With growing pressure and demand on aquatic ecosystems to provide water directly for drinking, agriculture and supporting industries and domestic use, the alteration of natural stream flow conditions is probably the biggest threat to the integrity of aquatic ecosystems (Poff et al., 1997; Bunn and Arthington, 2002; Nilsson and Renöfält, 2008; Ahn et al., 2018; Al–Jawad et al., 2019). Conflicts over the most essential services of aquatic ecosystems particularly rivers, between ecological and societal needs are increasing as global population and water demand rises (Tharme, 2003; Arthington et al. 2006). Surface water resources over southern Africa, especially river flow, have been projected to decrease by up to 35% by 2050 in rivers of the Limpopo catchment which incorporates the Luvuvhu catchment as a result of ongoing climatic change (Tharme, 2003; Nilsson and Renöfält, 2008; Kusangaya et al., 2013). Reduction in stream flow may lead to a change in perenniality of rivers from permanent to non-perennial, while permanent wetlands are becoming seasonal or temporary.

A consensus exists within the scientific community that rivers need to maintain and resemble the natural variation of flow conditions to sustain the ecological health and array of goods and services they provide to society (Poff et al., 1997; Richter et al., 1997; Bunn and Arthington, 2002; Richter, 2009). In recent times, water regulations have progressed to account for stream flow regimes that effectively protect freshwater ecosystems (Richter, 2009, Poff et al., 2010). This is because stream flow regime shapes many fundamental ecological characteristics of riverine ecosystems (Poff and Zimmerman, 2010; Arthington, et al., 2018). For example, rivers are classified as having excellent habitat structure based on their flow, and its resultant thermal and geomorphology signatures (Rivers-Moore et al., 2013). All elements of a flow regime (i.e., magnitude, frequency, duration, timing and rate of change) are important in structuring aquatic communities (Poff et al., 1997; Bunn and Arthington, 2002; Poff et al., 2018; Van Niekerk et al., 2019). Regardless of all these advances in generating trade-off strategies, which advocates for alternative and ecological water use scenarios, water policy and management have been implemented comparatively slowly. Thus, environmental flow regimes in rivers are currently being implemented in only a tiny fraction both at regional and catchment scales worldwide, with a vast majority of management applications only focusing on low flow (Richter et al., 1997; NWA, 1998).

Stream flow strategies that meet human needs while preserving and maintaining the ecological functioning of river systems have been passed into law in the South African National Water Act of 1998, through the declaration of the "ecological reserve" (Webb et al., 2018). The goal behind the ecological reserve is to negotiate for satisfactory trade-offs in water allocation among all users of the resource and the resource base itself (the river). Since the development of the environmental flow concept and methods in South Africa (Tharme, 2003; Salmaso et al., 2017), very few studies have assessed the institutional constraints to environmental flow implementation. Therefore, a sound evaluation of constraints to stream flow management should be based on specific information concerning management challenges and the implication between flow changes and ecological response (Kleynhans, 1996).

The aims of this study were to (1) determine the stream flow regime trend and anticipated impacts on aquatic organisms in the Luvuvhu River catchment, Limpopo province, South Africa; and (2) review local challenges affecting the sustainable management of river flows, especially in relation to the institutional capacity of the river management framework to provide environmental flows. We reviewed river management issues reported in the literature and contextualized them against an institutional capacity of Luvuvhu River management framework. This study also discusses the general ecological impacts of declining flow regimes and provides key management actions that can assist in overcoming stream flow management challenges.

5.2. Methods

Study Area

The Luvuvhu River catchment (LRC), Limpopo province, South Africa is currently subjected to major forms of stream flow alteration and its rivers play a significant role for both the human and ecological elements (Odiyo et al., 2015; Figure 5.1). Long-term annual rainfall and air temperature has not changed over the last 100 years in both the lower (Kruger National Park) and the upper (Levubu) sections of the Luvuvhu catchment (Figures S5.1 and

S5.2). Other studies in the LRC recognize the need to limit both water abstractions and changes to the river flow regimes by setting environmental standards that guard and maintain river ecosystem characteristics and functions (Jewitt and Garratt, 2004; Ramulifho, et al., 2019). The Luvuvhu River catchment is located in the Luvuvhu–Letaba Water Management Area, with a catchment size of approximately 5941 km^2 (Figure 5.1), with 14 quaternary catchments, with the main river channels being the Luvuvhu, Mutale, Mutshindudi and Dzindi Rivers (Jewitt and Garratt, 2004; Foord and Fouché, 2005). The Luvuvhu River catchment is important to forestry, macadamia, avocado and banana plantations in the headwaters, agricultural development in the valleys and lower slopes (western side) and rural and urban settlements (eastern side) (Angliss, 2001), while the rivers and the riparian vegetation of the Luvuvhu catchment are home to many bird and animal species (DWAF, 2012).

Elevation in the catchment varies from 1587 m in the west, where the Soutpansberg Mountains are located, to about 200 m in the eastern section of the catchment where the Luvuvhu River joins the Limpopo River (Heath, 1990). The catchment climate is considered semi-arid, with most of the rainfall occurring during summer, and is largely driven by the topography of the area (WRC, 2001). The mean annual temperature varies from 20 °C in the western section to 22 °C in the eastern section (Hope et al., 2004). The mountainous areas of the LRC receive the highest mean annual precipitation of 1800 mm as compared to 400 mm in the lowland areas. However, the mean annual precipitation for the entire catchment varies between 610 to 800 mm (Heath, 1990; Foord and Fouche, 2016), with a mean annual runoff of 519 million m^3 (Heath, 1990). The variability of streamflow has increased within the Luvuvhu River Catchment over an 86-year period, indicating that factors such as anthropogenic activities and reservoir development could be impacting on the river streamflow (Brown and Farrelly, 2009; Ramulifho, et al., 2019). Changes in stream flow regimes will affect the poor whose households’ livelihood activities are water-dependent.

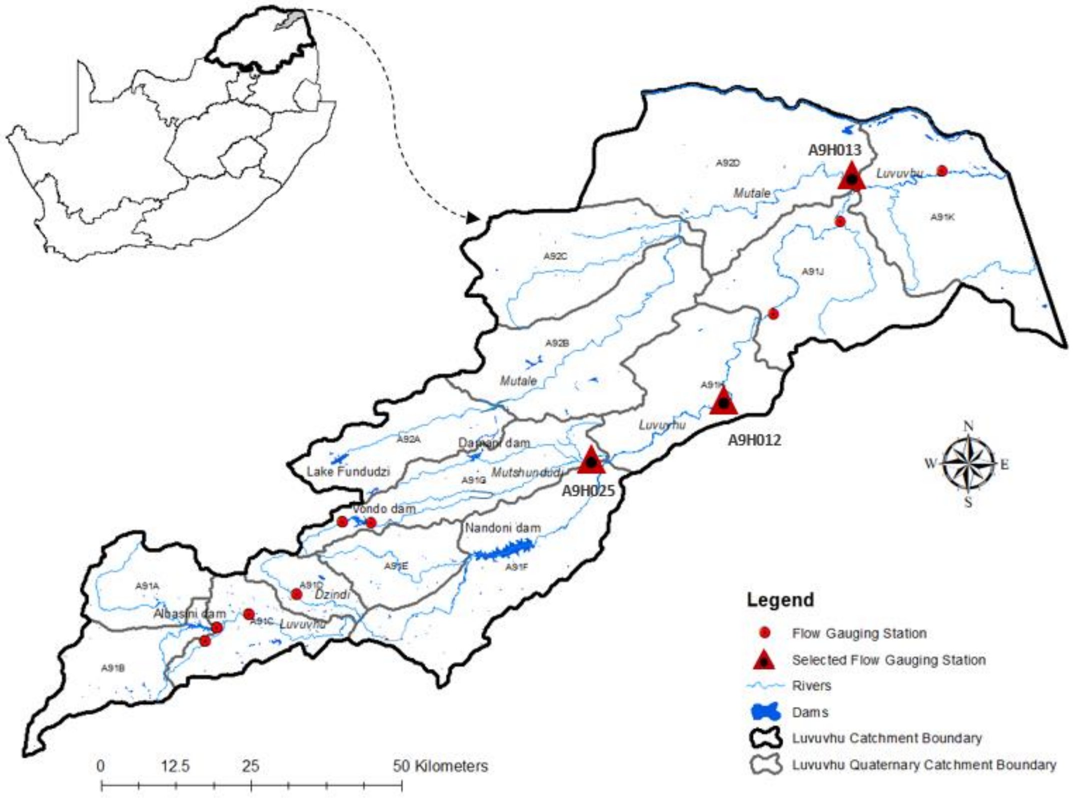

Figure 5.1: Map of the Luvuvhu River catchment highlighting the major dams, gauging stations and quaternary catchments.

Flow Data and Trend Analyses

Stations with long-term (>20 years) flow data that include the most recent flow periods were selected across the catchment (Table 5.1), with stations monitoring canals, pipeline and sluice gates being excluded from the analyses. Stations were inspected for completeness of stream flow data records and statistical anomalies. Gaps longer than one month were excluded from the analyses. We kept these stations in the analyses to account for best spatial variability. Only stream flow data was studied because it provides strong surrogacy for human impacts on stream flow changes and can be used to make deduction on climate change (Novotny and Stefan, 2007).

We fitted linear regression models to mean daily stream flow time series data using simple linear regression (SLR) to model temporal trends at three selected stations. A positive value of the slope indicates an increasing trend and a negative value a decreasing trend. Linear regression models and patterns in the temporal trends were run and visualized using the ‘lm’ and ‘ggplot’ function in R, respectively (R Core Team, 2017).

Table 5.1. Description of stream flow stations used in the study.

Flow Station	**Location**	**River**	**Lat (°S)**	**Long (°E)**	**Upstream Dam**	**Period**	**Years**	**Data Completeness (%)**	**Catchment Area (km²)**
A9H012	Mhinga	Luvuvhu	−22.86	30.88	Nandoni	1987–2019	32	95.4	1758
A9H013	Kruger	Mutale	−22.43	31.07	None	1988–2019	31	75.7	1776
A9H025	Matsika	Mutshundudi	−22.85	30.68	Thathe	1996–2017	23	78.0	387

Literature Search and Analysis

A search was conducted on the Web of Science and Google Search for local and international literature on stream flow regimes and water management strategies for the years between 1939 and 2019. In total, 480 publications were identified and those which were closely related to the topic and found to be peer-reviewed were included. These key words were used in the online search ‘environmental flow implementations and challenges’, ‘ecological impacts in rivers’, ‘Luvuvhu river catchment’, and ‘water resources management strategy’. We excluded studies that focused only on ecological management, ecological impact and water quality aspects with no relation to water and catchment management, respectively (Pollard et al., 2011).

5.3. Results

Stream Flow Changes

All three stream flow stations (Mhinga, Kruger and Matsika) highlighting a decreasing trend in stream flow volume (Figure 5.2; Table 5.2). These negative trends in long-term streamflow regime are significant for Kruger ($p = 0.016$) and highly significant for Matsika ($p < 0.001$). Stream flow volume is decreasing at 1 and 2 orders magnitude faster at Matsika than at Kruger and Mhinga stations (Figure 5.2). The figure shows that the mean daily stream flow trends in Matsika and Kruger are more likely to cross the zero flow intercept in near future (around 2030) than flow in Mhinga. This is because the greatest decreases in stream flow volume are rapidly occurring in small sub-catchments.

Table 5.2: Statistical results for flow trends analyses from the three selected stations flow. Trend significance level is indicated by * $p < 0.05$; ** $p < 0.01$.

Station	Y (Intercept)	Slope	Standard Errors	*p* Value
Mhinga	6.33	-1.413×10^{-5}	**4.476×10^{-5}**	**0.750**
Kruger	3.59	-6.185×10^{-5}	2.556×10^{-5}	0.016 *
Matsika	7.25	-3.281×10^{-4}	2.945×10^{-5}	<0.001 **

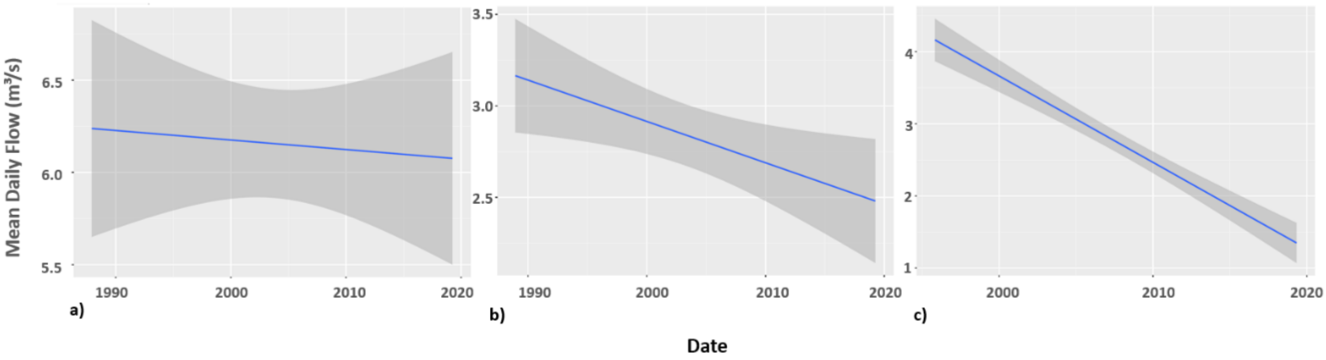

Figure 5.2: Fitted regressions of time series of streamflow at (a) Mhinga, (b) Kruger and (c) Matsika in the Luvuvhu catchment. Grey ribbons represent 95% confidence intervals for streamflow.

Possible Impacts on Aquatic Organisms Resulting from Changing Flow Regimes

Numerous studies have examined how aquatic organisms respond to changes in the quantity of water in river catchments around the world. Some dynamics on how fish and macroinvertebrate species are affected by changes in flow components is presented in Table 5.3. Modification of the natural flow regime has affected aquatic species in aquatic ecosystems worldwide, and the greater the departure from the natural regime the greater the loss of organisms and their ecosystem services (DWAF, 1997; Poff et al., 1997; Mwenge, et al., 2016). Some studies have reported that disturbed patterns of stream flow events possess critical implications for aquatic organisms, particularly fish and macroinvertebrate species, which determine their relative success and regulate ecosystem process rates (DWAF. 2007; Poff and Zimmerman, 2010). Studies have highlighted that the majority of fish and macroinvertebrate responses involved losing sensitive species as a result of altered flow magnitude when water flow decreases (Poff and Zimmerman, 2010). Reduction in stream flows in rivers and subsequent drying leads to rapid loss of fish and macroinvertebrates diversity as the habitat disappears (Table 5.3) (Poff and Zimmerman, 2010; Arthington, et al., 2018). Both increase and decrease in flow magnitude generally decreases macroinvertebrate and fish abundance and diversity in rivers. Rivers with physical disturbance from floods (and droughts) will have unstable substrates and tend to be characterized by low species diversity, and the biota found in such disturbed rivers often have life histories or behavioural characteristics of frequently disturbed environments (DWAF, 2001; Bunn and Arthington, 2002; King et al., 2004; Mwenge, et al., 2016).

Table 5.3: Summary of the main changes in ecological responses of fish and macroinvertebrate organisms in relation to the changes in the elements of streamflow regimes.

Changes in Flow Regime	Fishes	Macroinvertebrate
Magnitude	• Alteration of flow results in loss of sensitive species (Poff and Zimmerman, 2010). • Fish migratory changes both upstream and downstream due to too little water that impedes fish movement (MRC, 2010). • The magnitude of flood peaks can determine the degree of scouring mortality of fish egg (Poff et al., 2010).	• Alteration of flow results in loss of sensitive species (Poff and Zimmerman, 2010). • Greater magnitude of extremes causes life cycle disruption (Poff and Zimmerman, 2010). • Desiccation of macroinvertebrates (Hayes et al., 2018).
Frequency	• High frequency of flow, non-native species of fish may fail to establish (Poff et al., 2010). • Decreased reproduction and abundance of the native fishes (Stamou et al., 2018). • Influences the reproduction and mortality events of various species (Koma, 2010). • Decreased richness of endemic and sensitive species (Stamou et al., 2018). • Fish migratory changes such as increased upstream migration (Acreman, 2016)	• Increasing frequency of high flow disturbances, macroinvertebrate communities shift toward species adapted to high mortality rates, such as those having short life cycles and high mobility (Poff et al., 2010). • Increased variation results in life cycle disruption (Poff et al., 1997).
Duration	• Reducing the duration of low flows would not be expected to have a large effect on native fish (Poff et al., 2010). • Increase in abundance of non-native species (DWAF, 2001). • Increasing the duration of low flows could dewater habitat and damage native species (Poff et al., 2010).	• Decreased duration of floodplain inundation causes loss of floodplain specialists in mollusc assemblage (Poff and Zimmerman, 2010). • Increasing the duration of low flows would limit habitat available for invertebrate assemblages (Hayes et al., 2018; Stamou et al., 2018).
Timing	• The natural timing can prevent the establishment of non-native fish (Poff et al., 2010). • Loss of seasonal flow peaks disrupts cues for fish: spawning (Poff et al., 1997).	• Reduced survivorship of larval atyid shrimps following early summer spates (Bunn and Arthington, 2002). • Human-induced changes in timing may cause productive failure, stress and mortality (Koma, 2010).
Rate of Change	• The loss of seasonal flooding can promote success of non-native fish species (Poff et al., 2010). • Fish stranding and drifting (Meador et al., 2012; Brantley et al., 2015).	• Accelerated flood recession results in failure of seedling establishment (Poff et al., 1997). • Macroinvertebrate drift (Carlisle et al., 2014).

Challenges Facing the Implementation of Environmental Flows

Of the 480 local and international papers reviewed on stream flow regimes and water management strategies, 432 (90%) reported on natural flow regimes, methods of setting environmental flow standards, ecological consequences of altered flow regimes, management strategies and a wide range of political, economic, social and environmental issues surrounding water resources. Only 48 papers (10%) reported on terrestrial research and management that lack relevancy to stream flows and catchment management and were not included in this study. Five prominent challenges were found, which are: (i) absence of catchment management agencies/authorities (CMA), water user associations and water boards, (ii) lack of understanding of environmental flow benefits, (iii) limited financial budget, legal position and technical hydrological resources, (iv) lack of institutional and human capacity and (v) conflict of interest. These challenges facing sustainable stream flow management and the related river ecology have been evident within the LRC since the 1960s (Heath, 1990; Pollard et al., 2011). It is also apparent that declining stream flow is progressively degrading both the water quantity and associated fauna and flora within the catchment (Kleynhans, 1996).

Absence of Catchment Management Agencies (CMA), Water User Associations, and Water Boards

The absence of a catchment specific water resource governing structure in many situations is the baseline challenge in resource management. In the LRC situation, this causes the South Africa Department of Water and Sanitation (DWS) regional office to be the primary manager of the water resource (Heath, 1990). Legislative issues, human and financial resources limit the scope for many water management agencies operate as a water resource management body, as some policies are silent on water resource conservation and protection. It is only the CMA (in cooperation with water user associations and water boards) which is directed through the National Water Act, to collaboratively protect, allocate, conserve, manage and control water resources within a specific catchment (DWAF, 1997; DWAF. 2007). The main aim of setting up catchment management agencies is to decentralize responsibility for managing water resources so that water users and the public at large can play their part in managing and conserving the resource (DWAF, 1997; DWAF. 2007). Currently, it is now close to two decades since the encouragement for the formation of the water users association (which include municipal, industrial, agricultural and domestic users) and

CMA within the LRC (DWAF, 2012). No functioning structures are in place, making it hard to implement environmental flow management strategies and educate users on sustainable resource use.

Lack of Understanding of Environmental Flow Benefits

The importance of environmental flows in sustaining ecosystem services, local economies and other river-dependent organisms is still largely unrecognized and under-appreciated within the LRC (DWAF, 2012), while primary water uses for domestic and agricultural purposes still enjoy the highest priority. Very little environmental flow related benefits were recognized during the environmental and social impact assessment phases that were undertaken in 1997 for the then-proposed dams in the Luvuvhu and Lutanandwa Rivers (Heath, 1990). Environmental flows are perceived by many as more restrictive and political, serving only for officials who benefit from water resource management, as opposed to seeing them as developmental and conservation tool (Ström et al., 2012; Bejarano et al., 2017; Ahn et al., 2018; Al–Jawad et al., 2019). The widespread perception is that the impact of large water–resource developments on riparian communities is little understood, with continued misperception that environmental flows are intended to benefit primarily non–human species (Richter et al., 1996; Bejarano et al., 2017). Riparian communities prefers stream flow over reservoirs, exhausting all of the low flows in the river, particularly in the critically dry period of August to November, making it hard to implement sustainable stream flow actions in the LRC (Hope et al., 2004). Because of this, several studies suggest that the existing and potential impacts of aquatic resource loss are high (: Taylor and Cooke, 2012; Saltveit et al., 2001; Bejarano et al., 2017; Ahn et al., 2018; Al–Jawad et al., 2019). As long as communications about environmental flows remain centred on non-human benefits and conspicuously absent in the public media, these misperceptions of ecological reserves benefits will persist and it will be difficult to implement and conserve (Richter, 2009).

Limited Financial Budget, Legal Position and Technical Hydrological Resources

The challenges associated with the development and implementations of the LRC standards for environmental flow include financial, hydrological resources and legal constraints (Holzapfel et al., 2016). The way a CMA, water user association and/or water board is financed is of great significance for its success within the sustainable management of the catchment at stake (DWAF, 2012; Holzapfel et al., 2016), with potential to decelerate implementation of related water policies and procurement of critical and required hydrological information equipment (Hope et al., 2004; DWAF, 2012; Holzapfel et al., 2016). The absence of annual operating costs causes of high priority programmes to be financial sanctioned (DWAF, 2012). Inadequate technical tools for maintaining instream flow have been reported as huge constraints towards fully operating ecological reserves within the LRC (WRC, 2001; Jewitt and Garratt, 2004).

Lack of Capacity

A lack of capacity in terms of human resources in the government, with numbers being particularly low relative to the size of the system, limits performance (Angliss, 2001; Holzapfel et al., 2016). Shortage of dedicated environmental or hydrological staff and relevant department results in staff having to double up on their responsibilities and placement in positions for which they are not adequately trained (Baldwin et al., 2001). Coupled with limited management capacity, CMAs are unable to undertake and achieve their delegated mandates [Holzapfel et al., 2016).

Conflicts of Interest

The conflicting logjam for a priority use of water between major water supply schemes in upper catchments (e.g., Albasini government water scheme, Vondo regional water supply scheme and Luvuvhu irrigation scheme), sewage treatment works and the Malamulele regional water supply scheme in the lower catchment need to be harmonized within the LRC (Heath, 1990). It is also common that environmental flow management in many jurisdictions, regulation of surface water, groundwater and dams are not coordinated; therefore, action areas conflict and/or overlap (Richter, 2009). Due to lack of drinking water delivery in rural areas, infrastructure development and health, the government is further crippled by pressure to allocate adequate funds amongst these critical operational areas to eradicate backlogs in service delivery (Richter, 2009). Water managers are also hesitant to release bulk water for environmental purposes when other human uses could be jeopardized (Richter, 2009). Thus, implementing environmental flows in an unstable environment is a complex task, with conflict exacerbated by the need to recover water currently being used for other important purposes such as agriculture, industry and domestic supply, possibly bringing unintended economic and social impacts (Timusk, et al., 2016).

5.4. Discussion

Declining Stream Flow and Aquatic Organisms

This study found that natural flow volumes are currently declining significantly across the LRC, with the trend suggesting that flow is likely to cease in the foreseeable future. The decrease in mean flow volumes is apparently a human-driven process, since the decline is not consistent with the climatic conditions of the region (Figures S5.1 and S5.2). Rainfall and temperature in the Luvuvhu catchment have remained unchanged over the last 100 years (MacFadyen et al., 2018). Other studies in the LRC have reported the rate of water abstraction for commercial forestry and agricultural purposes as an immediate concern for the sustainable future of stream flow regimes (Kleynhans, 1996; Ramulifho, et al., 2019). Though our analysis was unable to place flow alteration in a more specific environmental context, several studies have shown that aquatic organisms are more likely to respond negatively to changes in hydrologic drivers (Poff et al., 2010; Poff and Zimmerman, 2010; Stamou et al., 2018). Catchment management strategies should acknowledge natural flow as the cornerstone in catchment management strategies (GNF, 2013), hence aiming to preserve the natural flow in rivers for the protection of natural freshwater ecosystems' biodiversity and the human livelihood and well-being that depend on these ecosystems (Arthington et al. 2006; Rivers-Moore et al., 2013; Quinteiro et al., 2018). In general, changes in stream flow regimes in the Luvuvhu catchment would not be favourable for the aquatic organisms and people who depend on this catchment for water. From a South African perspective, there is a huge potential for sustainable conservation of the LRC, given the simplicity of adopting widely applied tools such as Downstream Response to Imposed Flow Transformations (DRIFT) (King et al., 2004; Dallas and Rivers-Moore, 2014). DRIFT is a scenario-based approach that predicts and attempts to avoid severe impacts to flow, aquatic organisms and socio-economic factors of proposed water-resource developments on rivers (Bejarano et al., 2017).

Sustainable Catchment Management Prospects for the LRC

The main problem in the LRC is the absence of proper management institutions and strategies to address issues such as water allocation and conservation through an integrated management approach. Appropriate and capable river management institutions are needed and should be established within the LRC. These sentiments have been suggested by other studies done in this catchment (Kleynhans, 1996; Hope et al., 2004). River managers should set environmental flow regime standards and thresholds to achieve specific conservation objectives and support a diverse range of organisms, which otherwise is unattainable without stream flow management strategies (Richter et al., 1997; Dyson et al., 2003). Environmental flows should be set to resemble the natural flow regime of the river, thus enabling indigenous flora and fauna communities to prosper and provide their share of ecosystem services and benefits to humans (GNF, 2013; Bejarano et al., 2017). The choice for a best method to implement environmental flow regimes in catchment management is limited to merits and types of issues to be addressed (Tharme, 2003; Acreman and Dunbar, 2004; Sabzi et al., 2019). This is always influenced by a hydrological statutory authority (catchment management strategies or approach) to address water resources challenges and objectives (DWAF. 2007), as recommended following the process detailed in a white paper (DWAF, 1997) and by Department of Water Affairs and Forestry (DWAF) (DWAF, 2012). The national DWS recognizes that CMAs hold an important responsibility in hydrological landscape management, as they capture and synthesize essential water resource information as well as its strategic implementation for a sustainable future. The performance of these agencies that have a responsibility for the monitoring and managing river ecosystems in terms of their allocation of resources, implementation of actions and achievement of goals should continuously be evaluated and updated in a timely manner (DWAF, 2012; Irlich et al., 2017).

Implementation of sustainable catchment management strategies requires proper governance systems that ensure that CMAs gain adequate understanding of catchment water availability and land use impact within their water management areas (DWAF, 2001). To enhance stakeholders (local communities) engagement, environmental flow priority-setting and related benefits from their application should be communicated from a political and socio-economic water resource perspective (Pollard et al., 2011). A transparent, inclusive and well–coordinated stakeholder dialogue helps to popularize the notion that mankind does benefit from environmental and ecological flow regimes through a number of important silent services such as tourism, fishing, water retention and storage, and water supply and purification (DWAF, 1997; DWAF, 2001]. Therefore, as such, CMAs can then constrain human impacts on natural flow variability by better monitoring water withdrawal permits and dam licensing (DWAF, 2001; DWAF. 2007; Pollard et al., 2011).

Several approaches can be adopted to aid in conflict resolution and mediation skills, developing capacity, and raising funds towards implementation of environmental flow standards at catchment levels. Catchment conflicts over stream flow trade-off can be settled using a structured rational approach that values future goals and needs over perceptions, while harmonizing and mediation through the Water Tribunal and Courts of Law, as these institutions play an important role where serious water disputes arise. Institutional capacity to sustainably manage a LRC can be developed by raising awareness, identifying resources and capacity requirements to achieve compliance, collaboration with other catchment CMAs, increasing access to related environmental flow and ecosystem related information, and outsourcing capacity and resources that are available nationally for building capacity and assisting CMAs in achieving their overall targets (King et al., 2004; DWAF, 2007; King et al., 2008; Mwenge et al., 2016). An assessment of how the actual river health meets the stated vision, goals and objectives and the specific management actions that have been set should be carried out regularly (DWAF, 2012). The CMAs can raise funds through water–use (e.g., increasing tariffs for higher use and time-limited water abstraction licenses) and waste discharge charges and external financial investments (DWAF, 2007).

5.5. Conclusions

The development of scientifically credible catchment-wide flow management strategies and abstraction thresholds for rivers within the LRC would make a major contribution in minimizing the declining stream flow volumes due to water abstraction. Stakeholders will benefit from the biodiversity and essential ecological goods and services provided by the LRC ecosystem, while maximizing economic and social welfare in an equitable manner. The LRC will provide for human well-being in multiple ways, especially among rural poor communities living close to the river system (Foord and Fouché, 2005; Mwenge, et al., 2016). The implementation of these scientifically credible catchment guidelines for the protection and restoration of ecological integrity of rivers will squash all misperceptions that environmental flow thresholds are intended to benefit primarily fauna and flora (DWAF. 2007; Richter, 2009). For successful water resource management, it will always be necessary to have an understanding of how people and climate influence the distribution of daily flows. Monitoring and reporting should be prioritized to give regular accounts of the state of our rivers. Such a management exercise will mark the start of better policing of the LRC water resources and aid in moving towards the implementation of environmental flow strategies.

5.6. References

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Chapter 6: Summary and conclusions

6.1. Summary

The main objectives and findings of this study were:

(1) To quantify long-term changes in the stream flow regime of the Luvuvhu catchment.

All stream flow trend analyses point to declining stream flow volumes that are most pronounced during the wet seasons. Based on the first analyses of stream flow data that included the most recent flow periods, it was found the greatest decrease in stream flow volume occurring in Matsika and Kruger station. The second analyses of stream flow based on gauging station with temporal autocorrelation structure that reflect natural flow conditions, found that Tshino was the only gauging station with natural flow conditions, and therefore the only station analyzed for long-term flow trends. Residual plots suggested that flow at most of the stations is not natural. Further analyses of natural flow data showed that correlation between sub-daily flow and daily flow metrics is generally high (78%), while 7-day minimum and mean monthly flow decreased significantly more than maximum flows. Declining stream flow is not related to climatic changes as analysis of climatic data (rainfall and air temperature) in the last 35 years, showed no significant change in both rainfall and air temperature for the weather station closest to Tshino. The absence of catchment specific-management institutions and strategies to address issues such as water abstraction and allocation is one of the major problems associated with declining flow in the Luvuvhu catchment.

(2) To assess the influence of environmental variables on both mayfly and blackfly assemblage structure in the Luvuvhu catchment.

Mayfly richness was mostly driven by temperature and pH. Species richness decreased with increasing temperature as opposed to pH. Land cover also influenced mayfly richness. Variables that were important to mayfly assemblage structure included temperature, flow stream, elevation, land cover, and stone sizes. Generally, temperature was the most influential variable. Stream flow was the most common variable driving of blackfly richness and assemblage structure, with both richness and abundance increasing with flow.

(3) *To identify indicator species and change-point threshold of mayfly and blackfly species along important environmental gradients.*

Six mayfly species were identified as indicators taxa for temperature changes. These include *Nigrobaetis sp*., *Baetis sp*., *Euthraulus elegans*, *Dabulamanzia media* and *Baetis harrisoni* who's abundance declined with increasing temperature at a threshold of 19 °C, while *Caenis sp.* increased. Our field-based observation of 19 °C threshold for mayfly response is also supported by literature. Different blackfly species showed multiple change points along the conductivity and land cover gradients. *S.(M.) hargreavesi/chutteri* was the only indicator taxa identified for flow velocity gradient with a threshold response at 1.6 m/s.

6.2. Conclusion

This study has improved our knowledge and understanding of declining stream flow trends in the LRC. This study has also provided baseline information on the distribution of mayfly and blackfly communities. Given the compelling evidence of decline stream flow volume, it is also clear that development of catchment-wide flow management strategies and abstraction thresholds would make a major contribution in minimizing the rate and effect of declining stream flow volumes in rivers of the LRC. For the main channels that are already regulated, provision of environmental flows and restoration of habitat for aquatic species are the best solutions. Although dams have been removed in many regions (Cooper et al., 2013), because of the crucial importance of rivers in supplying water in these region, ongoing conflicts among different water users (between ecological and societal needs), is inevitable. The growing advocacy for dam re-operation to achieve environmental flows (Bunn and Arthington, 2002), is a possible harmonizing option for the LRC. For non-regulated rivers, the most effective option is to conserve and maintain their free-flowing condition, which enhances organism's capacity to resist climate change impacts and maximize the capacity for adaptation (Rivers-Moore et al., 2012). The other threat to both natural flow and aquatic macroinvertebrates community in the LRC is the transition from native vegatation to transformed lands (Evans, 2017). Conservation of native vegetation is one of the measures to improve the condition (stream morphology, water quality, and ecology) of LRC systems (Kleynhans, 1996). Awareness about the high ecological costs and impacts on biological resources by human activities should be promoted and initiatives towards conservation and sustainable management of the catchment should be incentivized (Kingsford, 2002).

In general, our investigation confirms the crucial role of stream flow and water temperature in structuring aquatic macroinvertebrates community assemblage and individual species. In addition, this study outlines the indirect and direct impact of anthropogenic activities and climate change on aquatic biota through changes in stream flow and water temperatures. While water temperature appeared to be rising, stream flow is declining. Increasing temperatures may support eurythermic species (*Caenis sp.)*, while ultimately threatening cold-adapted species, which comprise the bulk of mayfly and blackfly diversity. Because natural vegetation correlated positively to high species richness, possiblely due to the input of allochthonous organic matter (Siegloch et al., 2014), this study reinforces the importance of maintaining natural vegetation areas for conservation of biodiversity and water resources. Furthermore, the data reinforce the use of mayflies as environmental indicators, since many genera were sensitive to landscape changes (caused by either human or natural activities) and responded to environmental gradients.

Future studies should include temperature logging to provide continuous data for long-term catchment moinitoring. Such data on their own would be highly valuable to the fields of ecology and taxonomy, but if they are analysed in relation to variables such as flow and water temperatures over a range of habitats and environments, the value of the studies would increase exponentially. There is need for extensive study focusing on the distribution, abundance and tolerance of the main indicator species in these rivers. While only two target groups were analysed in this study, similar studies conducted on additional taxa from more rivers across the catchment would allow for a much needed reference database. Perhaps incorporating more sites from thjis catchment into existing river monitoring programmes carried out by the government, such as the River Health Programme would also be beneficial. Future studies can also use the findings from this study which links specific species to specific thermal and hydrological thresholds in rivers of the Luvuvhu catchment to develop environmental flow targets. This will ensure that stream flow sustain ecological processes and associated animal and plant communities in this region.

6.3. References

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Appendices - Figures

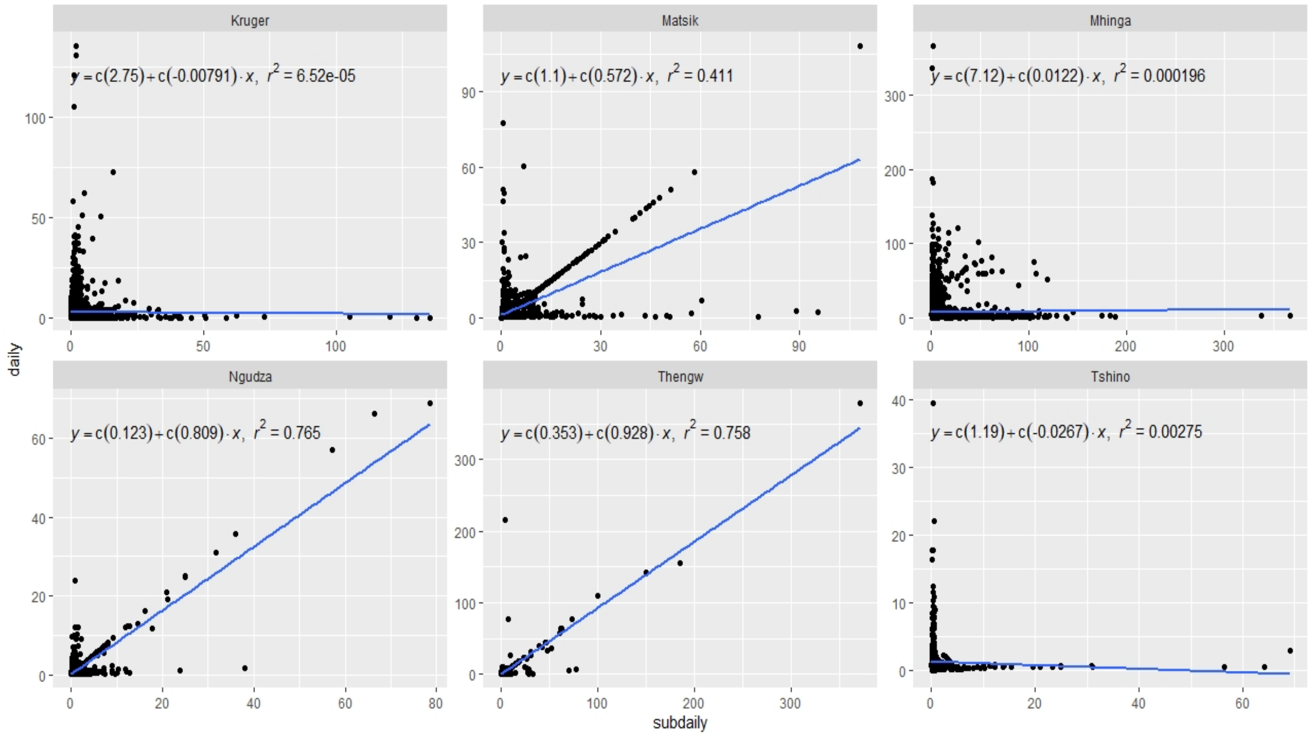

Figure S2.1: Scatter plots and regressions between mean daily flow and mean daily flow calculated using sub-daily flow at six gauging stations.

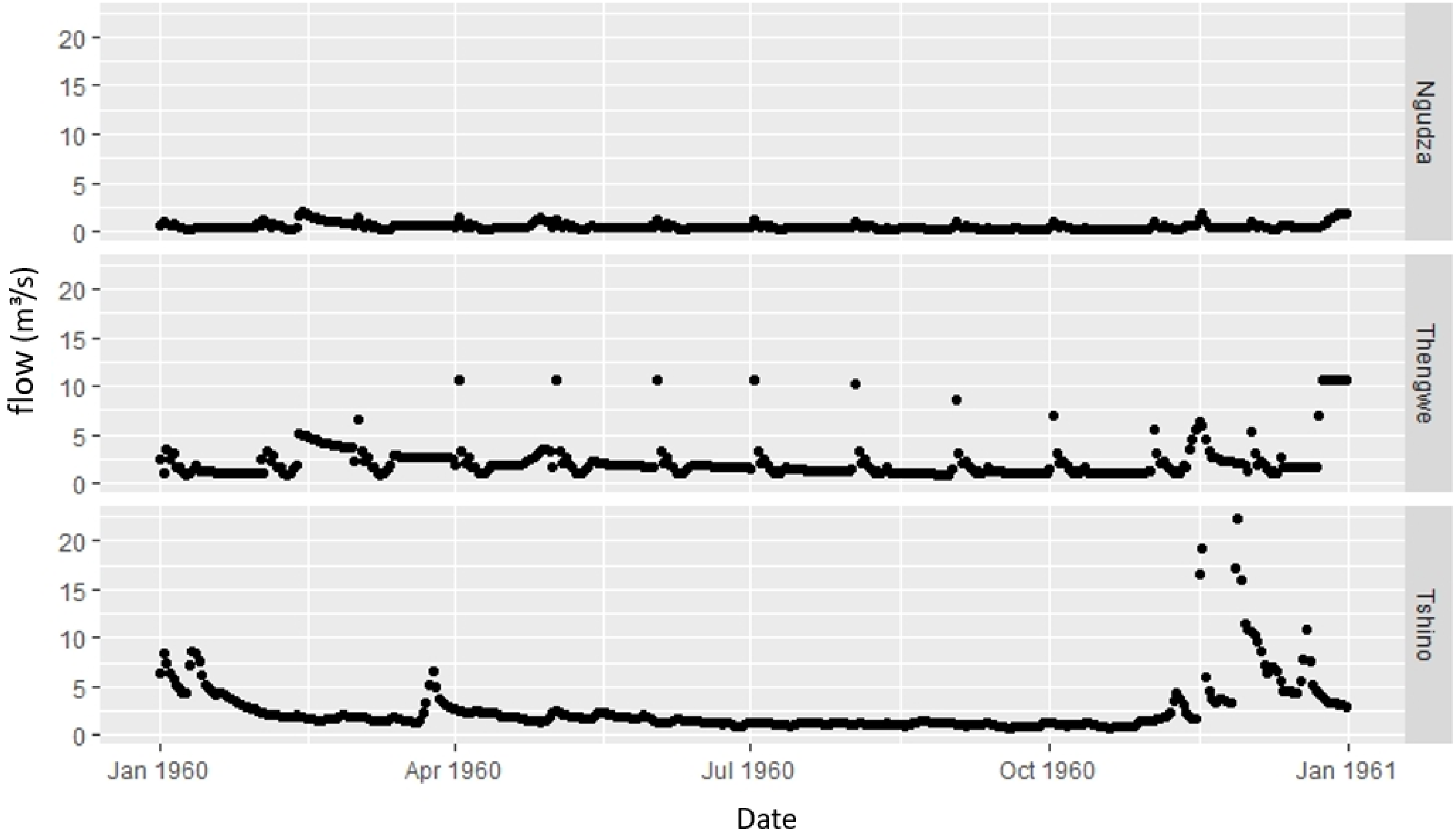

Figure S2.2: Time series of daily stream flow in 1960 at Ngudza, Thengwe and Tshino. Flow peaks are evident during regular intervals at Ngudza and Thengwe.

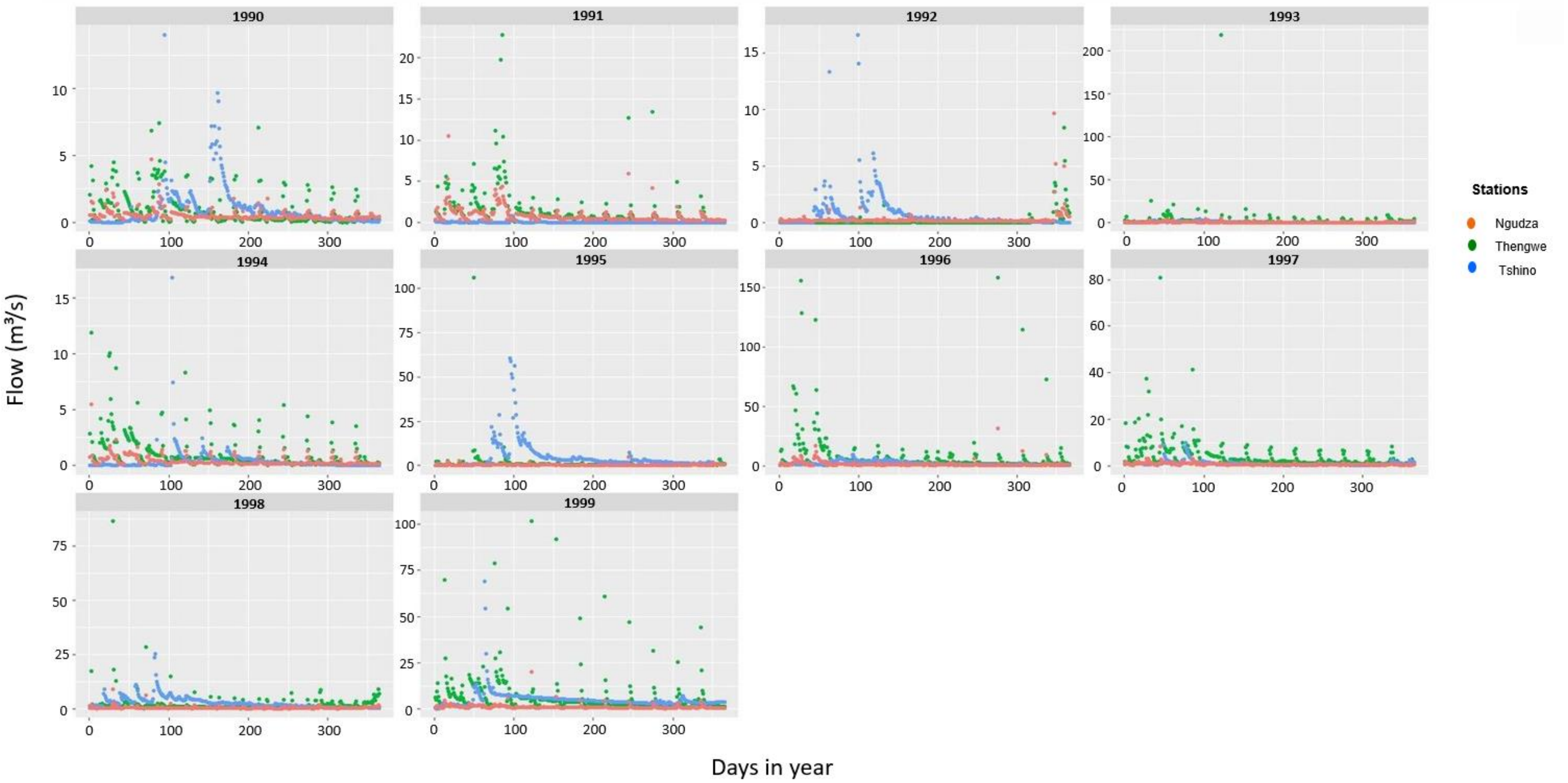

Figure S2.3: Time series plots of daily stream flow between 1990 and 1999 at Ngudza, Thengwe and Tshino. Flow peaks are evident during regular intervals at Ngudza and Thengwe.

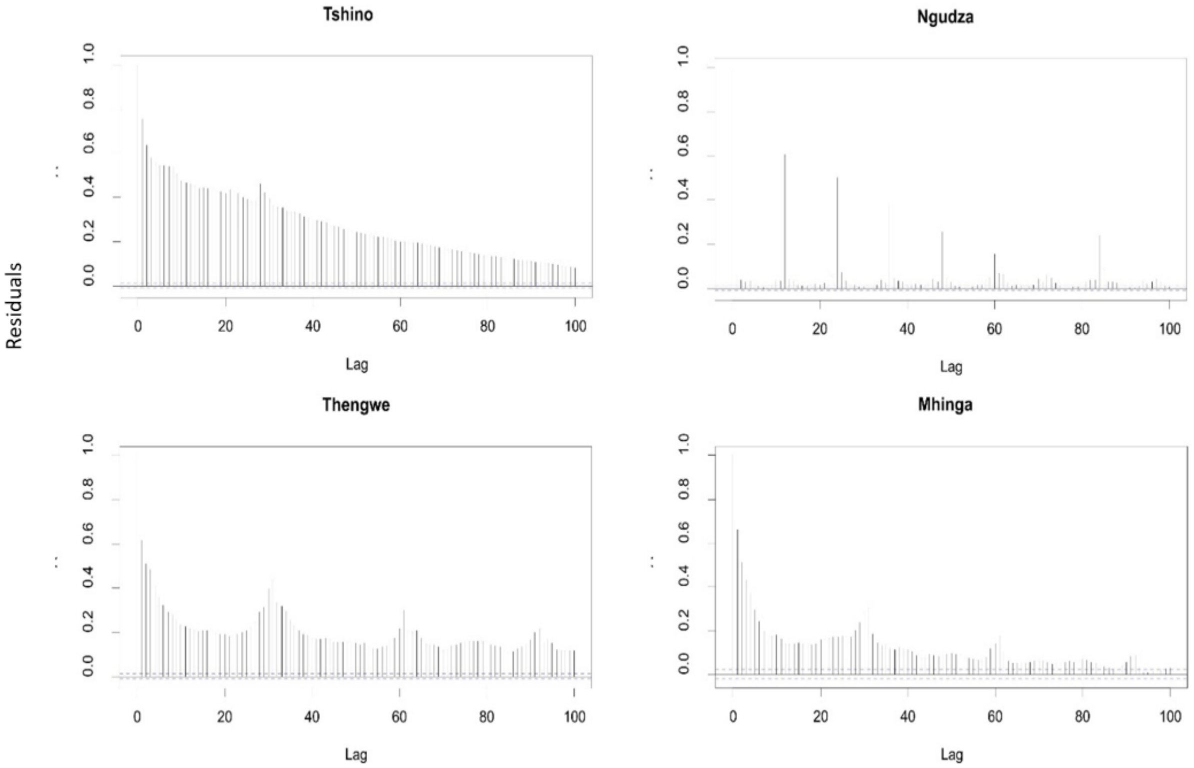

Figure S2.4: Autocorrelation plot of residuals derived from a linear regression without the inclusion of an autocorrelation residual structure. Note the peaks at regular interval for gauging stations at Ngudza, Thengwe and Mhinga. This contrasts with the residual structure at Tshino which show serial autocorrelation between closely related days.

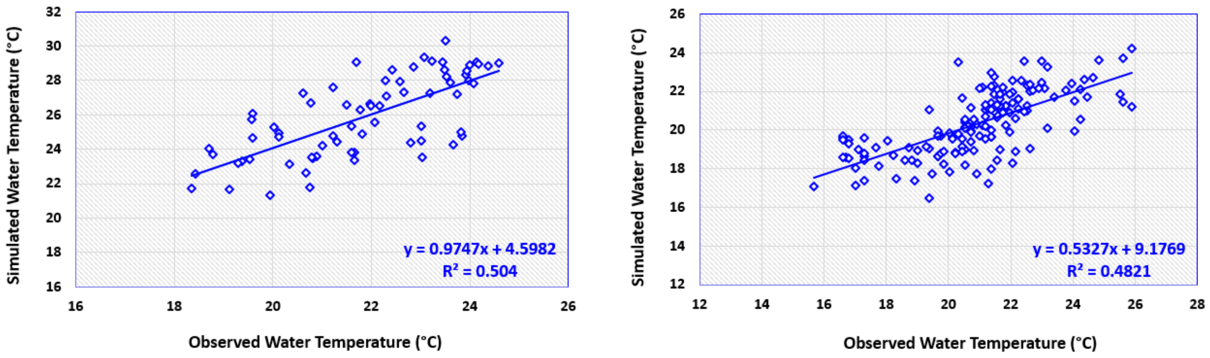

Figure S2.5: Relationship between observed and simulated water temperature in the Mutale (left) and Luvuvhu River (right).

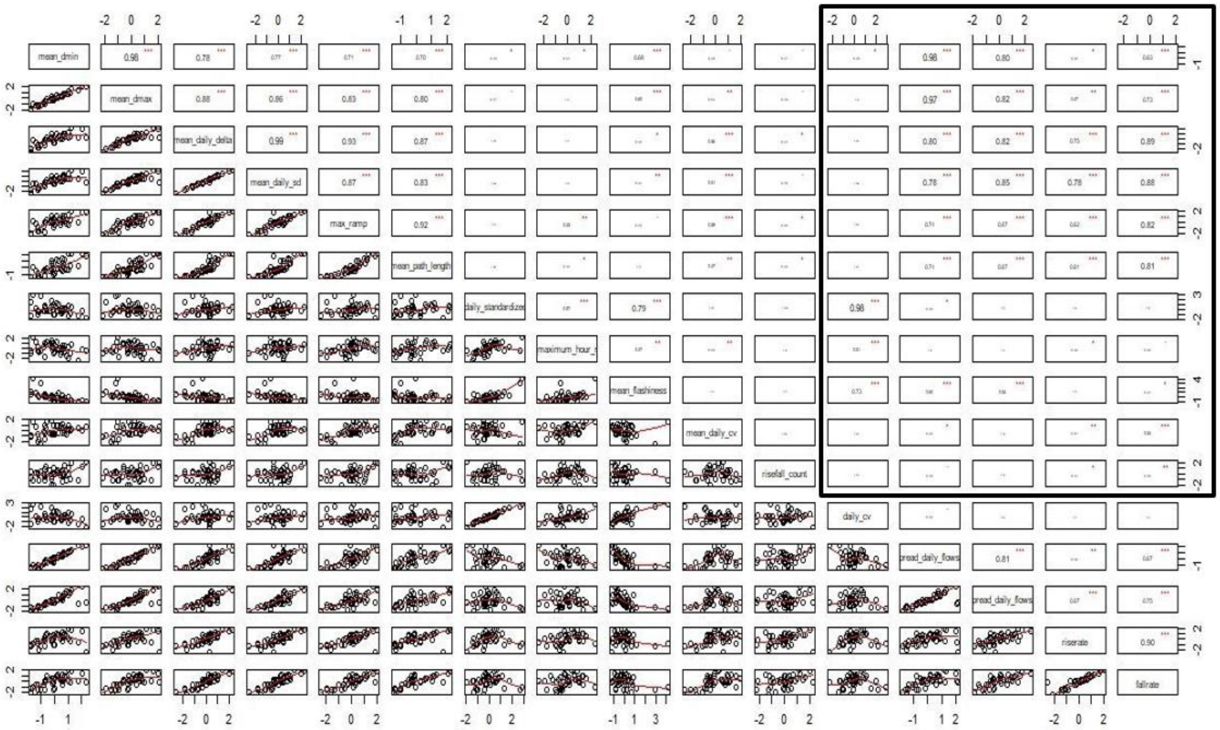

Figure S2.6: The correlations between hydrologic metrics of sub-daily flow regime versus daily metrics with the score and significance value. The rectangular block represent the area with coefficient of determination of correlation between sub-daily flow and daily flow metrics.

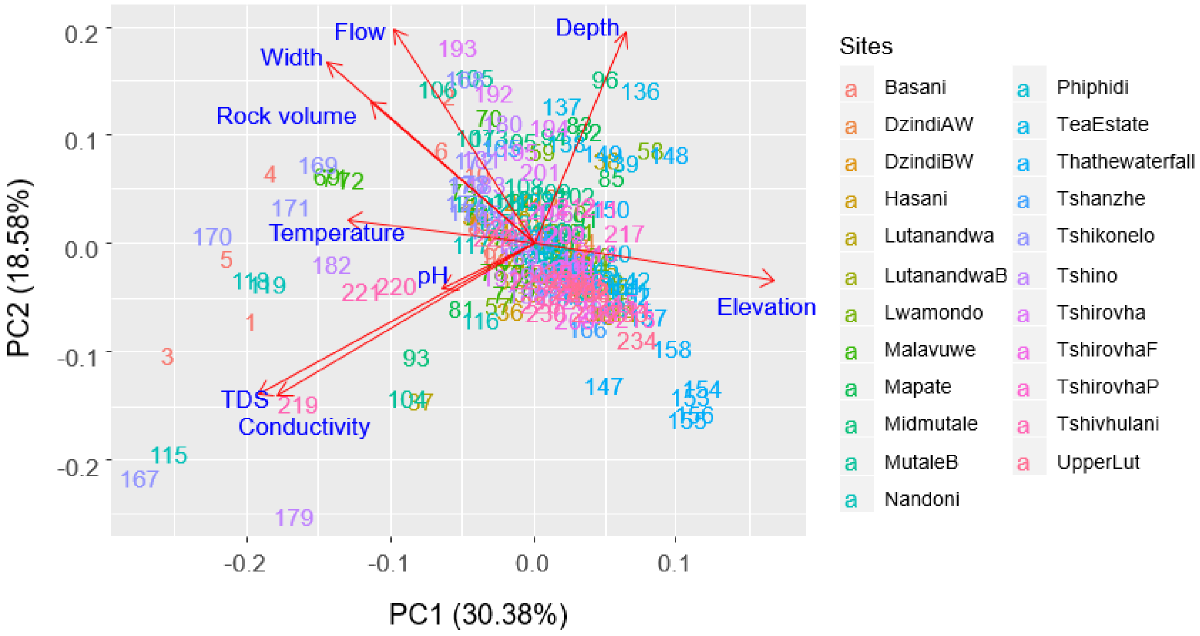

Figure S3.1: Principal Component Analysis ordination of the 23 study sites and nine environmental variables sampled in the Luvuvhu river catchment.

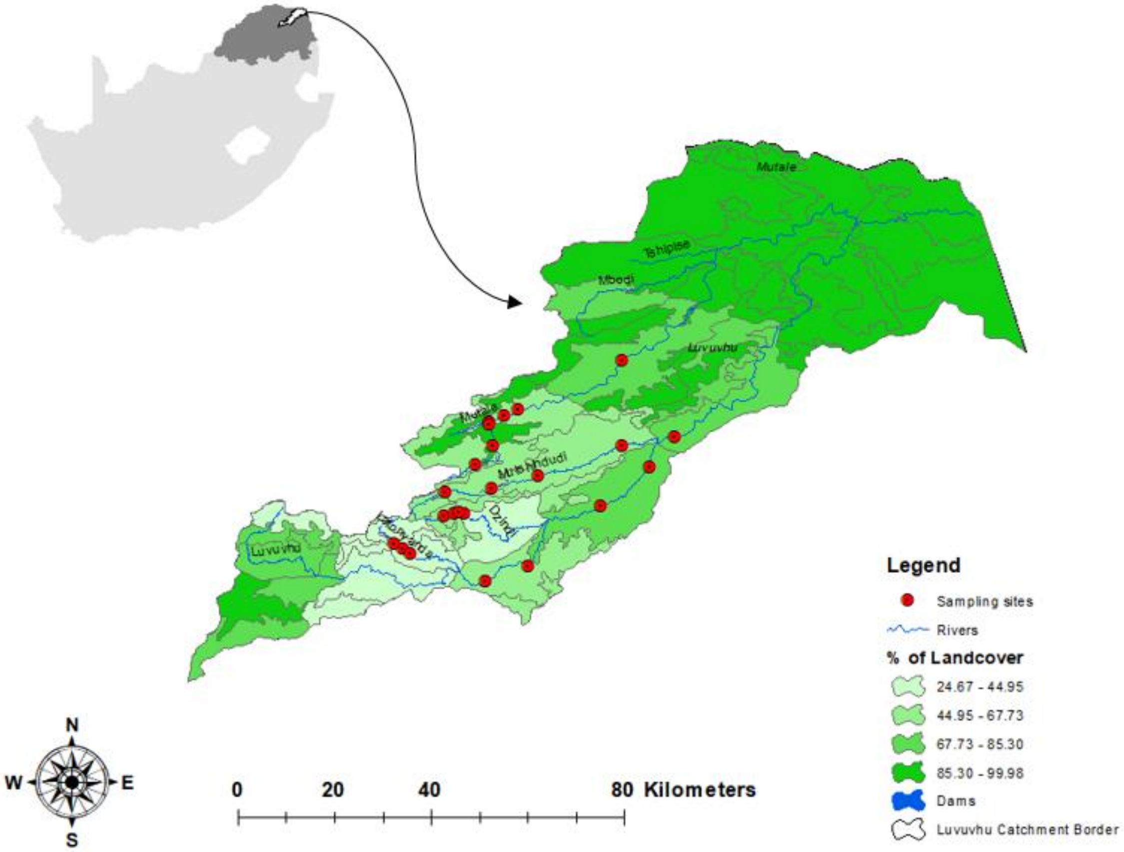

Figure S3.2: The percentage of natural vegetation cover shown at a quinary scale in the Luvuvhu catchment.

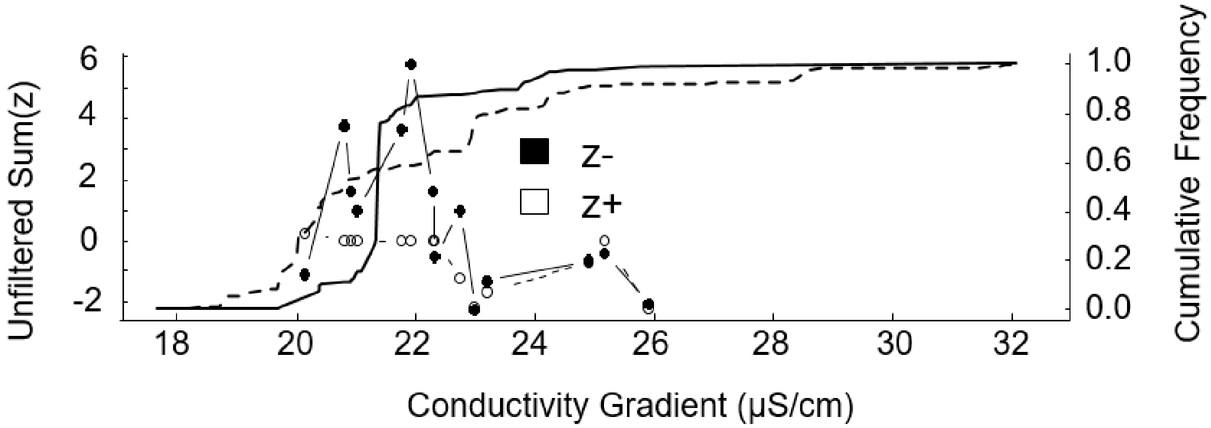

Figure S4.1: TITAN sum (z−) and sum (z+) values for all possible change points of blackfly community in response to a conductivity gradient. Solid and dashed lines represent the cumulative frequency distribution of change points among 100 bootstrap replicates for sum (z−) and sum (z+), respectively.

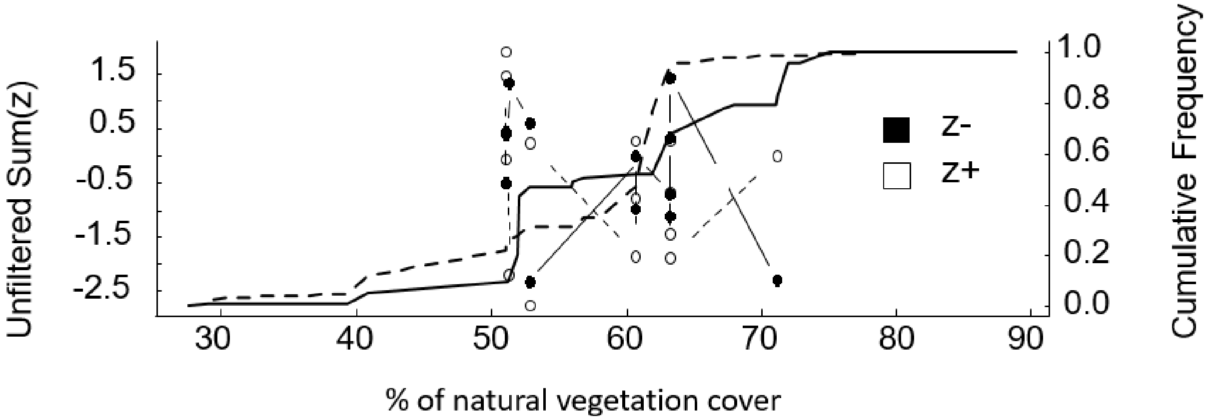

Figure S4.2: TITAN sum (z−) and sum (z+) values for all possible change points of blackfly community in response to a land cover gradient. Solid and dashed lines represent the cumulative frequency distribution of change points among 100 bootstrap replicates for sum (z−) and sum (z+), respectively.

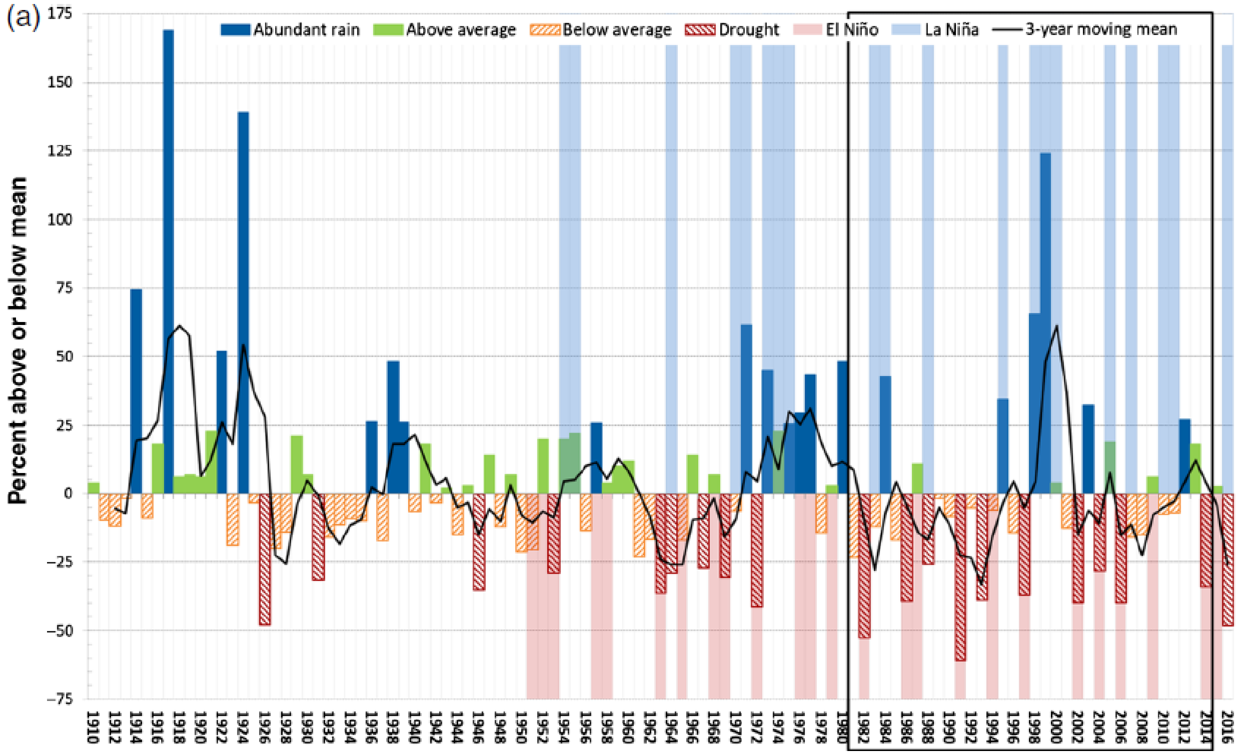

Figure S5.1: Unchanging long-term patterns of (a) annual of Kruger climate records (MacFadyen et al., 2008).

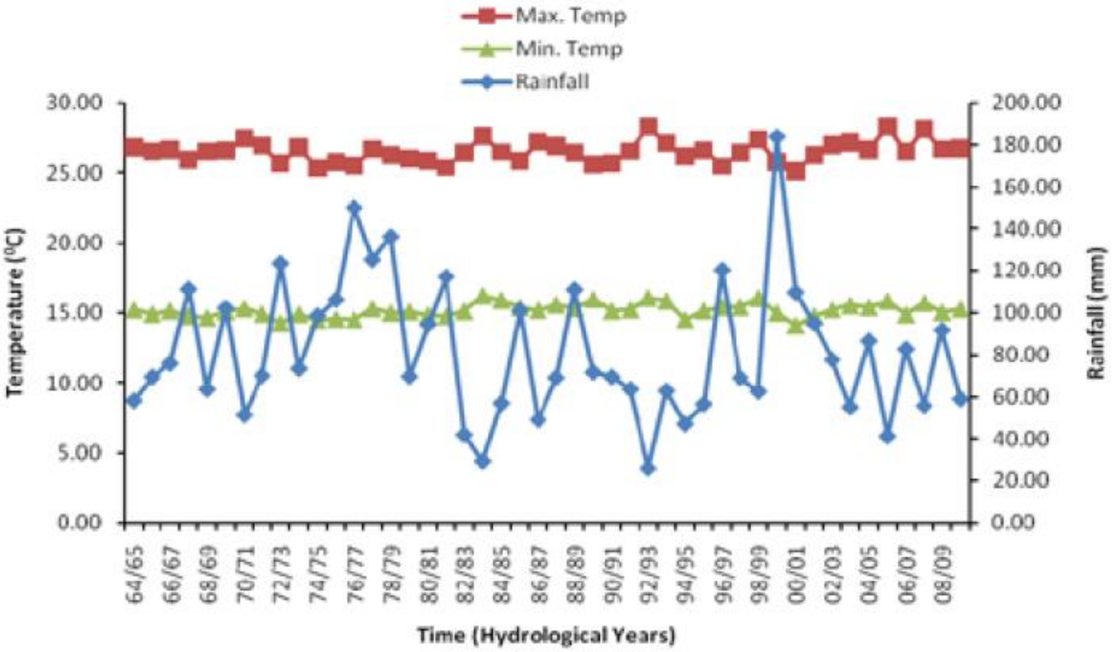

Figure S5.2: Unchanging rainfall in relation to minimum and maximum temperatures in the Levubu area (Nkuna and Odiyo, 2016).

Appendices – Tables

Table S2.1: Regression of mean daily flow derived from sub-daily flow and mean daily acquired from DWS for five stations in the Luvuvhu catchment.

Site	Station number	Term	Slope Estimate	Std.Error	Coefficients' test statistics	P Value	Adjusted R^2	Days with both daily and sub-daily flow
Kruger	A9HO13	Mean Flow	-0.007	0.023	-0.349	0.726	-0.000	1875
Matsika	A9H025	Mean Flow	0.571	0.013	42.804	0.000	0.411	2623
Mhinga	A9H012	Mean Flow	0.005	0.024	0.213	0.831	-0.000	4289
Ngudza	A9H003	Mean Flow	0.123	0.078	0.243	0.549	0.765	5266
Thengwe	A9H004	Mean Flow	0.927	0.030	30.653	1.97×10^{-94}	0.757	302
Tshino	A9H001	Mean Flow	-0.026	0.018	-1.422	0.155	0.001	736

Table S2.2: Attributes for hydrologic data used in predicting water temperature (WT) and the coefficient of determination.

River	WT observation station	Flow station	Air Temperature station	Distance between WT and Flow station	Difference in Elevation	Number of days of Observation	R^2
Luvuvhu	Tshikonelo	Mhinga	Punda Maria	17km	27m	70	0.504
Mutale	Mutale Bridge	Kruger	Thohoyandou	90km	357m	155	0.482

Table S2.3: Sub-daily (#) and daily (*) flow metrics and their description (adapted from Bevelhimer, 2015).

Metric (m^3/s)	Description
Daily minimum#	Lowest measured flow during a 24-h period.
Daily maximum#	Highest measured flow during a 24-h period.
Daily delta#	Difference between daily minimum and daily maximum represents the amount of daily flow change.
Daily standard deviation#	The common statistical calculation of the 24 hourly flow values. Like daily range, daily standard deviation is an indicator of degree of habitat change.
Maximum hourly ramp rate#	The greatest hourly incremental change in flow during a 24-h period.
Daily path length#	The sum of the absolute values of hour to hour changes in flow with time.
Rise and fall counts difference#	Difference between the number of hours of rising and falling flow as determined with each pair of consecutive flow values.
Daily standardized delta#	A variation of the percent of total flow metric, this metric is calculated as the daily delta divided by the daily mean over each 24-h period.
Annually standardized delta#	An alternative to the daily standardized delta that is standardized by dividing by the mean annual daily flow instead of by each day's mean flow.
Coefficient of variation#	Daily standard deviation divided by the daily mean.
Maximum hourly ramping rate#	Maximum daily ramp rate divided by the mean annual daily flow.
Richards–Baker flashiness index#	The daily path length of flow oscillations divided by the daily mean over each 24-h period. Higher values indicate greater stream flashiness or more rapid variation in flow
Daily coefficient of	Calculated from daily flow averages for each year and then averaged across years.

variation*	
Spread in daily flows one*	Difference between the 90th and 10th percentile of the flow data divided by the median flow for the entire record.
Spread in daily flows two*	Difference between the 25th and 75th percentile of the flow data divided by the median flow for the entire record.
High flood pulse count*	Average number of flow events per year exceeding a threshold equal to the 75th percentile value for the entire flow record.
Rise rate*	Average rate of positive changes in flow from one day to the next divided by median daily flow.
Fall rate*	Average rate of negative changes in flow from one day to the next divided by median daily flow.

Table S3.1: Sites, mayfly abundance, richness, vegetation cover and average scores of environmental variables measured at sampling sites in the Luvuvhu catchment between December 2016 and February 2018.

Site Name	Samples	Altitude	Temp	Flow	Depth	Width	TDS	pH	Conductivity	Natural Cover %	Total Mayfly abundance recorded	Mayfly Species Richness recorded
Thathe waterfall	12	1022.94	19.21 ±3.18	1.30 ±0.90	10.81 ±4.77	03.34 ±1.70	11.88 ±4.50	06.83 ±0.95	18.37 ±7.50	91.44	6	3
Tshirovha	12	665.26	20.22 ±3.38	2.05 ±1.20	14.75 ±5.96	14.08 ±7.33	13.02 ±2.91	07.23 ±0.82	18.15 ±6.71	63.21	337	13
Midmutale	12	667.52	22.58 ±3.39	1.83 ±1.18	20.73 ±10.30	12.26 ±1.23	13.81 ±3.17	07.05 ±0.27	21.29 ±4.67	63.21	314	12
Mutale Bridge	12	651.96	20.48 ±3.65	2.61 ±1.56	15.86 ±7.08	18.25 ±5.32	13.35 ±3.51	06.46 ±0.30	21.00 ±5.47	63.21	361	11
Tea Estate	12	876.59	19.18 ±3.06	2.25 ±1.25	16.04 ±5.85	08.58 ±1.32	12.51 ±3.53	06.90 ±0.59	17.53 ±7.69	51.33	911	11
Tshivhulani	12	475.71	21.39 ±3.08	1.27 ±0.58	15.33 ±6.67	09.87 ±0.81	19.97 ±10.26	07.69 ±0.20	27.63 ±11.33	60.73	209	12
Malavuwe	12	484.24	21.71 ±3.44	1.58 ±1.02	12.31 ±2.92	19.66 ±4.87	15.93 ±5.46	07.61 ±0.34	25.38 ±8.63	60.73	822	12
Lwamondo	12	796.01	17.96 ±1.47	1.93 ±1.00	14.90 ±7.09	07.73 ±1.11	13.49 ±3.33	07.22 ±0.43	20.88 ±5.12	51.12	1040	11
Mapate	12	688.13	20.31 ±1.81	2.12 ±0.91	15.91 ±7.01	09.82 ±1.32	13.26 ±3.71	07.58 ±0.37	19.73 ±6.66	30.64	634	11
Lutananda	12	716.14	20.08 ±2.95	1.86 ±0.87	14.59 ±5.86	06.00 ±1.06	15.93 ±6.01	07.33 ±0.45	2.51 ±8.13	27.59	919	13
Tshino	12	577.86	21.96 ±3.54	1.68 ±0.91	15.12 ±5.71	11.58 ±2.16	17.19 ±9.64	07.95 ±0.46	27.15 ±14.97	52.85	1110	15
Nandoni	12	483.78	23.05 ±2.23	1.89 ±0.77	16.06 ±7.97	12.16 ±3.11	21.62 ±14.54	07.91 ±0.60	33.60 ±22.82	71.18	358	10
Basani	12	466.14	24.31 ±3.93	2.21 ±0.22	14.85 ±10.75	18.41 ±3.04	24.01 ±16.34	07.61 ±0.66	31.29 ±22.09	71.18	565	12
Tshikonelo	12	457.22	23.60 ±4.07	2.56 ±1.39	15.47 ±6.22	22.29 ±3.77	22.00 ±14.16	07.72 ±0.26	34.43 ±21.97	72.90	479	12
Tshirovha potholes	09	934.02	18.15 ±2.83	1.37 ±0.66	14.81 ±5.61	11.11 ±2.41	14.63 ±1.02	06.64 ±0.55	22.87 ±1.64	91.44	270	12
Tshirovha forest	09	622.38	18.17 ±2.76	1.60 ±1.17	13.33 ±6.61	11.25 ±0.96	14.49 ±0.78	06.61 ±0.32	22.97 ±1.19	63.21	36	8
Dzindi above Waterfall	09	731.65	19.66 ±2.04	1.68 ±0.82	16.95 ±4.87	09.75 ±0.43	13.99 ±0.59	07.52 ±0.29	21.74 ±1.08	51.12	523	11
Dzindi below Waterfall	09	690.49	19.23 ±2.01	1.89 ±1.01	14.08 ±3.37	11.88 ±0.70	14.14 ±0.62	07.53 ±0.25	22.30 ±1.31	51.12	475	10
Phiphidi	09	605.32	20.57 ±2.76	1.31 ±0.60	13.00 ±3.80	12.62 ±0.48	13.74 ±0.92	07.19 ±0.14	21.73 ±1.03	60.73	429	13
Lutananda Bridge	09	651.19	19.93 ±3.17	2.01 ±0.95	14.02 ±4.16	09.25 ±0.96	14.96 ±2.64	07.56 ±0.20	22.27 ±1.75	27.59	689	11
Hasani	09	532.27	21.60 ±3.88	1.39 ±0.83	11.34 ±2.29	14.75 ±1.39	13.78 ±0.97	07.85 ±0.15	21.02 ±1.62	52.85	224	8
Tshanzhe	09	547.53	22.03 ±3.92	1.10 ±0.81	16.98 ±6.24	09.25 ±3.15	13.36 ±0.99	07.22 ±0.18	20.79 ±1.71	78.93	28	7
Upper Lutananda	09	745.57	19.15 ±3.72	1.31 ±0.69	14.89 ±4.21	05.25 ±0.43	13.96 ±1.21	07.45 ±0.55	25.54 ±6.98	27.59	302	9

Table S3.2: The name, genus and abundance of the 19 mayfly species collected during the 12 months sampling period in the Luvuvhu catchment.

Name of Species	Genus name	Family name	Species occurrence frequency	% of species occurrence	species abundance	% of species abundance
Acanthiops varius	Acanthiops Waltz & McCafferty, 1987	Baetidae	12/23	52.17	123	1.11
Afronurus barnardi	Afronurus Lestage, 1924	Heptageniidae	22/23	95.65	914	8.28
Afroptilum sudafricanum	Afroptilum Gillies, 1990	Baetidae	1/23	4.35	1	0.01
Baetis.harrisoni	Baetis Leach, 1815	Baetidae	20/23	86.96	1276	11.56
Baetis sp.	Baetis Leach, 1815	Baetidae	23/23	100.00	2734	24.76
Caenis sp.	Caenis Stephens, 1835	Caenidae	20/23	86.96	308	2.79
Centroptiloides bifasciatum	Centroptiloides Lestage, 1918	Baetidae	2/23	8.70	13	0.12
Cheleocloeon sp.	Cheleocloeon Wuillot & Gillies, 1993	Baetidae	19/23	82.61	354	3.21
Cloeon sp.	Cloeon Leach, 1815	Baetidae	1/23	4.35	12	0.11
Dabulamanzia media	Dabulamanzia Lugo-Ortiz & McCafferty, 1996	Baetidae	21/23	91.30	1666	15.09
Demoulinia crassi	Demoulinia Gillies, 1990	Baetidae	2/23	8.70	7	0.06
Elassoneuria trimeniana	Elassoneuria Eaton, 1881	Oligoneuriidae	5/23	21.74	52	0.47
Euthraulus elegans	Euthraulus Barnard, 1932	Leptophlebiidae	22/23	95.65	1232	11.16
Nigrobaetis sp.	Nigrobaetis Novikova & Kluge, 1987	Baetidae	21/23	91.30	847	7.67
Pseudocloeon glaucum	Pseudocloeon Klapálek, 1905	Baetidae	14/23	60.87	272	2.46
Pseudocloeon sp.	Pseudocloeon Klapálek, 1905	Baetidae	3/23	13.04	13	0.12
Pseudoponnota maculose	Pseudopannota Waltz & McCafferty, 1987	Baetidae	18/23	78.26	287	2.60
Pseudoponnota sp.	Pseudopannota Waltz & McCafferty, 1987	Baetidae	3/23	13.04	4	0.04
Tricorythus discolor	Tricorythus Eaton, 1868	Tricorythidae	18/23	78.26	926	8.39

Table S4.1: Names, geographic locations and summary of physo-chemical variables from the 23 samplings sites in the Luvuvhu Catchment River between December 2016 and February 2018.

Site Name	Latitude	Longitude	Samples collected	Stream flow	Flow depth	Rock size	Width	Temperature	TDS	pH	Conductivity	Elevation
Thathewaterfall	-22.9	30.37	12	2.46	18.03	2781.15	19.14	24.32	25.79	7.68	34.90	398.14
Tshirovha	-22.82	30.4	12	1.85	15.70	2257.33	9.78	19.22	14.17	7.55	21.92	731.65
Midmutale	-22.81	30.42	12	1.94	14.02	2202.65	11.86	19.15	14.19	7.52	22.33	690.49
Mutale Bridge	-22.79	30.45	12	1.30	11.67	2510.81	14.75	21.61	13.78	7.86	21.02	461.29
Tea Estate	-22.95	30.32	12	1.96	15.07	1591.34	6.09	20.01	16.16	7.35	24.88	716.14
Tshivhulani	-22.92	30.49	12	2.09	13.63	1126.35	9.33	19.89	15.09	7.57	22.30	651.19
Malavuwe	-22.86	30.64	12	1.96	15.36	3496.45	7.77	17.98	13.52	7.23	20.91	796.01
Lwamondo	-22.99	30.31	12	1.70	12.77	2129.49	19.52	21.78	15.83	7.64	25.16	435.27
Mapate	-22.99	30.35	12	2.13	16.03	2103.72	9.74	20.19	13.48	6.56	20.15	688.13
Lutanandwa	-23.05	30.24	12	1.81	22.00	2195.93	12.51	22.33	13.01	6.99	20.04	662.52
Tshino	-23.11	30.39	12	2.62	16.38	2230.00	20.29	22.38	14.46	7.04	22.76	651.96
Nandoni	-22.97	30.6	12	1.93	15.48	2605.83	12.48	23.10	22.71	7.89	35.32	457.78
Basani	-22.9	30.7	12	1.36	13.33	1318.84	12.63	20.53	13.77	7.19	21.76	605.32
Tshikonelo	-22.84	30.74	12	2.35	16.46	2616.90	8.70	18.68	12.80	6.90	17.95	876.59
Tshirovha potholes	-22.86	30.4	9	1.52	11.41	2083.65	3.45	19.33	11.46	7.03	17.72	1022.94
Tshirovha Forest	-22.82	30.4	9	1.16	17.21	1988.15	9.25	22.04	13.36	7.22	20.79	547.53
Dzindi above Waterfall	-22.99	30.33	9	2.48	15.58	2311.24	22.31	23.62	21.76	7.72	34.05	457.22
Dzindi below Waterfall	-22.98	30.34	9	1.85	15.68	2511.31	11.68	22.01	16.76	7.89	26.45	479.86
Phiphidi	-22.94	30.4	9	2.50	16.28	2993.20	15.21	20.50	12.60	7.17	17.66	665.26
Lutanandwa Bridge	-23.06	30.25	9	1.45	12.64	1080.84	11.35	17.77	14.64	6.64	23.19	622.38
Hasani	-23.08	30.47	9	1.51	15.80	1534.51	11.08	17.96	14.65	6.59	22.98	934.02
Tshanzhe	-22.7	30.64	9	1.24	14.75	2231.41	9.85	21.32	19.85	7.70	27.37	475.71
Upper Lutanandwa	-23.04	30.22	9	1.39	14.88	1393.70	5.28	19.02	14.00	7.43	25.92	745.26

Table S4.2: The total abundance and richness of the seven blackfly species at all 23 sampling sites during the 12 months sampling period.

Site Name	***S.(E.) damnosum***	***S.(M.) adersi***	***S.(M.) hargreavesi/chutteri***	***S.(M.) hirsutum***	***S.(M.) medusaeforme***	***S.(M.) vorax***	***Simulium (pomeroyellum)***	**Abundance**	**Richness**
Thathewaterfall	1	16	8	0	1	1	6	33	6
Tshirovha	22	13	23	0	6	9	16	89	6
Midmutale	1	1	9	0	0	3	3	17	5
Mutale Bridge	29	2	8	0	0	0	24	63	4
Tea Estate	1	8	35	2	23	12	13	94	7
Tshivhulani	0	1	0	0	0	2	0	3	2
Malavuwe	2	11	4	0	2	0	12	31	5
Lwamondo	0	5	8	0	5	1	12	31	5
Mapate	23	5	1	0	12	2	13	56	6
Lutanandwa	8	1	2	0	8	4	17	40	6
Tshino	2	12	18	0	1	2	2	37	6
Nandoni	13	15	29	0	1	0	1	59	5
Basani	24	12	47	1	13	0	1	98	6
Tshikonelo	0	7	7	0	0	0	3	17	3
Tshirovha potholes	1	3	1	2	7	2	10	26	7
Tshirovha Forest	9	39	66	44	96	179	18	451	7
Dzindi above Waterfall	0	7	16	15	22	16	6	82	6
Dzindi below Waterfall	3	3	4	2	13	2	6	33	7
Phiphidi	2	2	5	0	2	2	1	14	6
Lutanandwa Bridge	12	4	6	0	7	0	21	50	5
Hasani	0	0	0	0	0	0	0	0	0
Tshanzhe	0	0	0	0	0	3	0	3	1
Upper Lutanandwa	0	0	3	5	2	0	6	16	4

Table S4.3: Threshold Indicator Taxa ANalysis (TITAN) individual taxa results from the conductivity and land cover analyses. The low number of pure and reliable taxa resulted in no filters for both conductivity and land cover (Number of z- taxa = 0 and Number of z+ taxa = 0).

Blackfly Species	**Z. Median (Conductivity)**	**Filter (Conductivity)**	**Z. Median (Land cover)**	**Filter (Land cover)**
S.(E.).damnosum.s.l.	3.10	0	2.13	0
S.(M.).adersi	1.86	0	2.27	0
S.(M.).hargreavesi/chutteri	1.90	0	2.16	0
S.(M.).hirsutum	1.64	0	1.26	0
S.(M.).medusaeforme	1.69	0	2.02	0
S.(M.).vorax	1.73	0	1.28	0
Simulium.pomeroyellum	2.59	0	2.39	0