Spatio-temporal change in riparian woodlands of the Kruger National Park: drivers and implications

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Abstract

Verbal accounts, supported by limited ground-based and satellite images, reveal decreasing riparian woodland and a loss of large trees along the rivers of the Kruger National Park (KNP) over the last century. These habitats occupy a tiny fraction of the park's surface area but fulfil critical ecological functions and provide several ecosystem services. Little research has, however, focused on riparian woodland dynamics across the park. Here a multi-decadal time-series analysis of riparian woodland extent was conducted to identify trends in extent and possible drivers of riparian woody vegetation change. Aerial and satellite imagery (1936 to 2018) was used to measure changes in the extent of riparian woodland tree cover for 18 approx. 10 km long sites along five perennial and nine non-perennial rivers in KNP. This change was compared in a multivariate time-series with river flow and rainfall data from nearby gauging and weather stations, respectively. Particular attention was paid to cumulative flow effects, as well as the frequency and magnitude of large infrequent disturbances (LIDs) such as droughts and floods, which regulate the depth of the water table and may manifest as a physical disturbance. Tree cover fluctuated over the time period and the trajectory of change varied between sites. Most sites (n=11) experienced a decline in overall tree cover over the period while 14 showed a downward trend, six significantly. Overall tree cover increased at six sites, three of which showed an increasing trend (one significantly). There tended to be proportionately higher tree cover loss per year at sites with higher median tree cover. It appears that tree cover decreased substantially at a number of sites following the mega-flood event of 2000 and subsequent large floods over the last decade. It was not possible to generalise responses for the different sites, no doubt because of varying geology, flow regimes and vegetation characteristics at each site, resulting in differing responses to aspects of river flow and rainfall. Peak flow and maximum rainfall events, however, were the strongest significant association with decreases in riparian tree cover, indicating that floods are potentially the biggest drivers of tree loss. Flow variability and cumulative rainfall appear to significantly influence woodland expansion. The initial findings from this study should prompt increased attention to riparian habitats through fine-scale, detailed work aimed at further understanding the dynamics of these systems and determining thresholds for conservation concern in an attempt to ensure persistence of these important ecosystems.

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To Courtney Hallink, thank you for your unwavering motivation. This degree was infinitely easier alongside a fellow Masters candidate. Finally, to my parents, Robert and Sara, thank you for your continued support, financially, in particular, to pursue this degree, at a time when securing funding otherwise has become challenging.

“Whatever the water touched was riparian: that moist layer of air and rich earth along the shore was an Eden for many forms of life. Some drowned in a daily flood, while those that knew how, thrived.” – Brian K. Friesen, At the Waterline

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Introduction

Riparian zones are disproportionately species-rich per unit area, compared to surrounding habitats and supply several critical ecosystem services such as interception of nutrients and pollutants from upland and acting as biological corridors (Gregory et al. 1991; Naiman & Decamps 1997; Naiman et al. 2005). Their high ecological value and vital role in general ecosystem functioning render them invaluable in terms of biodiversity conservation and wider ecosystem integrity. As a consequence, there is concern over the persistence of riparian vegetation in South Africa's largest terrestrial protected area, the Kruger National Park (KNP), because repeat fixed-point photos and limited aerial imagery show a massive decline in the extent of the riparian woodlands over the past couple of decades (D Thompson *pers. comm.*). Furthermore, the rivers flowing through the park have been modified and are increasingly under strain due to growing anthropogenic pressures outside the park's boundaries (Mackenzie et al. 2003; O'Keefe & Rogers 2003; Pollard et al. 2011). Changes in climate, particularly in extreme events and seasonal variability, are also likely to intensify (van Wilgen et al. 2016), with potential consequences for riparian ecosystems. While the effects of the exceptional floods of 2000 have been widely documented (see Rountree et al. 2000; Heritage et al. 2001; Smithers et al. 2001; O'Keefe & Rogers 2003; Parsons et al. 2005, 2006; Ayres 2012), they appear to be spatially and temporally restricted with limited historical evaluation across the park. Identifying and quantifying changes, and assessing the potential drivers thereof, may reveal the sensitivity of these riparian systems to changing environmental conditions driven by climate and enforced by anthropogenic disturbances. This is critical to the adaptive management of these ecosystems and in fulfilling broader biodiversity and ecosystem functioning conservation goals and may be applicable to riparian systems in savannas elsewhere.

Because riparian systems are the interface between aquatic and terrestrial systems, they are functionally distinct from surrounding areas (Gregory et al. 1991; Naiman & Decamps 1997). The biological communities in riparian zones arise from the complex dynamics between climate, hydrology, geomorphology, fire and anthropogenic factors, at scales ranging from a pool or riffle to an entire catchment (Hughes 1988; Carter & Rogers 1995; Naiman & Decamps 1997; Stanford 1998). Riparian vegetation structure and composition are principally influenced by access of plant roots to the water table, which is usually high in riverine habitats. Additionally, vegetation is influenced by broader landscape processes including fluvial disturbances, groundwater and soil chemistry, flood tolerance and geomorphology and landform stability (Carter & Rogers 1995; O'Connor 2001, 2010b; Naiman et al. 2005). These are maintained by processes which occur at different spatio-temporal scales compared to surrounding systems (Naiman & Decamps 1997; Reinecke et al. 2013). Riparian physiognomy is also shaped by organisms which occupy these habitats (Naiman & Decamps 1997). In sub-Saharan savannas, riparian areas are often characterised by relatively dense vegetation comprising large, evergreen trees, in sharp contrast to the surrounding upland vegetation (Monadjem 2005; Monadjem & Reside 2008), making them structurally and floristically intermediate between tropical forest and savanna (Hughes 1988).

Beyond their high biodiversity value, riparian systems also fulfil numerous ecosystem services critical to ecosystem functioning within and beyond the riparian boundary, and of benefit to humans (Naiman &

Decamps 1997; Soman et al. 2007; King & Pienaar 2011). Ecologically, these ecosystems act as biological corridors, providing habitat connectivity critical to many species, and facilitating ecological processes and transfer of energy (Clarke 2003; Pettit & Naiman 2007a; Seavy et al. 2009; King & Pienaar 2011). Riparian vegetation acts as a buffer to disturbances such as flooding and fire to upland areas and stabilises riverbanks, reducing erosion and soil loss (Naiman & Decamps 1997; Hood & Naiman 2000; Clarke 2003; Merritt et al. 2010; King & Pienaar 2011). Furthermore, riparian vegetation aids in trapping upland pollutants, fertilisers, sediments, wastewater and pesticides, preventing their spread to areas downstream (Gilliam 1994; Hood & Naiman 2000; Naiman et al. 2005; Soman et al. 2007). Riparian vegetation also facilitates functioning in the aquatic environment by providing shade, regulating temperature, controlling flow and trapping debris which provides habitats and refuges for aquatic fauna (Naiman & Decamps 1997; Clarke 2003; Gordon et al. 2004; Naiman et al. 2005; Pettit & Naiman 2007a; Merritt et al. 2010; Kotzé 2015). In the terrestrial component, trees intercepting nutrients leads to long-term accumulation of woody biomass in riparian zones increasing shade, cover and foraging material (Naiman & Decamps 1997; Hood & Naiman 2000; Naiman et al. 2005). Riparian areas are frequented by various taxa which utilise the zone for feeding (Monadjem & Reside 2008; Moe et al. 2009; Kotzé 2015) and for access to drinking water (Naiman & Decamps 1997). For example, African riparian areas are critical to water-dependent antelope such as waterbuck (*Kobus ellipsiprymnus*) and nyala (*Tragelephus angasii*a) and elephant (*Loxodonta africana*) make use of riparian areas and edges for feeding year-round but especially in the dry season (Gaylard et al. 2003; O'Connor et al. 2007; Estes 2012; Robson et al. 2018).

From an anthropogenic perspective, riparian habitats are culturally, aesthetically and economically important (Hood & Naiman 2000; Nilsson & Berggren 2000; Clarke 2003; Merritt et al. 2010; King & Pienaar 2011). People living near riparian areas or in lower reaches of catchments benefit from riparian zones; hydrological control by intact vegetation and absorbent soils mitigate flooding and are usually the least impacted ecosystems in severe drought, often buffering the effects on other systems downstream (Clarke 2003; Scholes et al. 2003; Naiman et al. 2005; Schachtschneider 2014). The riparian areas of KNP offer high tourist value which translates into important conservation funds. In a study conducted in the most widely-visited region of KNP, Turpie & Joubert (2001) found that over a quarter of the road network traversed rivers and half of the respondents felt that large riverine trees were important features within riparian habitats. The study concluded that roughly 30% of KNP revenue could be attributed to river systems alone owing to visitor preference and utilisation. This is important given the substantial financial contribution KNP makes to the national park suite in South Africa (Freitag-Ronaldson & Foxcroft 2003).

Ecosystem structure and functioning change in space and time, sometimes through successional processes leading to a gradual shift, or through infrequent but impactful disturbance events (Gregory et al. 1991; O'Connor 2010b). Due to their unique nature within landscapes and the importance of these systems, riparian vegetation change associated with river dynamics has been widely assessed, particularly in relation to large floods and drought, and increasingly to reduced flows and abstraction and shifting flow patterns due to human impacts. Riparian zones are typically highly variable and unpredictable ecosystems, subject to flooding, erosion, alluvial deposition and drought (O'Keefe &

Rogers 2003; Naiman et al. 2005). Flooding and periods of low flow are critical for virtually all riparian species and maintain ecological integrity (O'Keeffe & Davies 1991; Poff et al. 1997; Bendix & Hupp 2000; Hood & Naiman 2000; Gordon et al. 2004; Milan et al. 2018). The timing, duration, frequency, magnitude and intensity of flooding are the primary aspects of river flow which shape riparian vegetation structure and associated biota, through interactions with fluctuating water levels, channel structure and substrate characteristics (Hughes 1988; Poff et al. 1997; O'Connor 2001; Rogers & O'Keeffe 2003; Naiman et al. 2005; (Hughes et al. 2008; Merritt et al. 2010; O'Connor 2010b; Reinecke et al. 2013). Flooding can remove plants through abrasion or erosion and/or undercutting of substrata, or by sheer force (Naiman & Decamps 1997). Consequently, the topography and geomorphic template supporting riparian woodlands are constantly changed by stream discharge (flow), creating a unique and shifting spatio-temporal mosaic (Gregory et al. 1991; Naiman & Decamps 1997; Stanford 1998; Milan et al. 2018).

The return interval, duration and intensity of such disturbances is important. Annual floods may only impact seedling establishment while intermediate frequency flooding may impact ecosystem structure on a scale of decades. Long-term, large disturbances may alter vegetation structure for several centuries (Brinson 1990). Conversely, periods of prolonged drought or low flow conditions may induce stress and dieback in many riparian plant species (O'Connor 2001, 2010b), despite their inherent adaptions to fluctuating water availability. Water is a limiting resource and its availability impacts plant competitive ability, biomass, resistance to pathogens and herbivores and thus overall vegetation structure (Merritt et al. 2010; Milan et al. 2018). Variable river discharge leads to a highly distinct and dynamic structure within the landscape, supporting only species which are able to cope with significant disturbances (Gregory et al. 1991; Naiman et al. 2005; Schachtschneider & Reinecke 2014). Riparian trees, in particular, must possess physiological and morphological adaptations to resist these inherent environmental stresses (Naiman & Decamps 1997). In southern African savannas, certain large, long-lived species are able to grow in areas susceptible to variable flow, deposition of substrate, periods of drought, increased flow and inundation due to adaptations such as leaf-folding, stem flexibility, stem buttressing and adventitious root structures (Naiman & Decamps 1997; Breen et al. 2000; Rogers & O'Keeffe 2003; Naiman et al. 2005).

KNP has 31 548 km of rivers within its boundaries (O'Keefe & Rogers 2003), including six large perennial rivers (Luvuvhu, Shingwedzi, Letaba, Olifants, Sabie and Crocodile) and many smaller, non-perennial rivers and streams. These drain seven sub-catchments and three primary river catchments *viz*. Limpopo, Komati and Olifants. The flow regimes of most rivers regionally are highly unpredictable over time with a large coefficient of variation (CV) resulting in vegetation communities which are dynamic and varied (Rogers & O'Keeffe 2003; Reinecke et al. 2013). In KNP, river characteristics, catchment areas and flow regimes, varied geology and climate gradients across the park have given rise to variable riparian vegetation (Gaylard et al. 2003; O'Keefe & Rogers 2003; Rogers & O'Keeffe 2003; Milan et al. 2018). From the perspective of conserving ecosystems associated with longitudinal river systems, KNP is unfortunately positioned, being orientated north-south while most rivers in the region flow west-east (**Figure 1**), draining into the Indian Ocean. As a consequence, many of these rivers emanate outside the Park making them susceptible to a variety of anthropogenic alterations (O'Keeffe & Davies 1991;

Gaylard et al. 2003; Roux et al. 2008; Pollard et al. 2011). Forestry, mining, urbanisation and irrigation for agriculture have impacted all of the main rivers in KNP to an extent that their flow regimes have apparently been severely modified, such that only one main river – the Sabie, is considered *truly* perennial (Pollard et al. 2011). This modification is thought to reinforce extreme events and flow variability, leading to a deterioration in quality and quantity of biota and certainly in the last two decades, altering riparian communities on some rivers (Hill et al. 2001; State of Rivers Report 2001; O'Keefe & Rogers 2003; Rogers & O'Keeffe 2003; Parsons et al. 2006; Fouche & Vlok 2010; Pollard et al. 2011; Petersen et al. 2014; Marnewick et al. 2015).

KNP provides some of the most pristine and extensive, albeit threatened, examples of riparian woodland in the region, affording the opportunity to assess the influences of land use and other anthropogenic impacts upstream, as well as natural drivers, on riparian woodland integrity. Despite this, scant attention has been given to the status of riparian zones in KNP. Only the Sabie River has been extensively studied from various perspectives. Of those studies that have explored riparian woodland dynamics and even in relation to flow and rainfall, most have typically assessed the effects of single large events, such as the floods of 2000 or drought of 1991/2. Little work, even elsewhere, has assessed the *historical trends* in riparian extent, which is useful for determining future management decisions (Vanak et al. 2012). This project used KNP as a case study to assess changes and associated drivers of riparian tree cover (woodland). Specifically, this study sought to elucidate changes in riparian tree cover over time and its links to river flow and rainfall. Based on the anecdotal evidence, I hypothesised an overall decline in riparian woodland extent which I predicted to be primarily due to large infrequent disturbances (LIDs) such as drought and especially flood events. Considering that river flow has been found to be greatly reduced in recent decades due to increased demand and conflicting land uses further upstream (Breen et al. 2000; State of Rivers Report 2001; O'Keefe & Rogers 2003; Pollard et al. 2011), LIDs have likely been exacerbated by anthropogenic pressures, although these were not quantified of directly compared in the study. Given the highly variable nature of the riverine areas within KNP, underpinned by different weather, geology, disturbances and flow regimes (Carter & Rogers 1995), it was predicted that both tree cover change and the environmental variables responsible thereof would vary strongly at the local scale. Historical repeat time-series aerial and satellite imagery (dating as far back as 1936) was used to detect changes in riparian woodland vegetation cover across 18 distinct sites across the park, using trees on the macro-channel bank as an indicator. Vegetation cover changes were assessed in relation to concurrent flow and rainfall records to assess potential relationships. Because of the diverse nature of the riparian systems in the park, the impacts between different river order, primary geology and flow perenniality were therefore also considered.

Methods

Study area and site selection

The Kruger National Park is located in north-eastern South Africa (**Figure 1**), covering an area of 1.86 million ha of low-lying savanna, comprising several ecozones, vegetation types and landscapes resulting in high biodiversity (Gertenbach 1983; Freitag-Ronaldson & Foxcroft 2003; Jacana Maps 2003;

Mabunda et al. 2003). The park experiences predominantly summer rainfall and given its size and orientation, experiences a large range in annual rainfall (MAP of 375–925 mm) with a generally increasing trend from north to south (and high inter-annual variation in MAP), and a mean of 47 rain days per annum (Venter et al. 2003; Zambatis 2003; SANParks 2018). Most precipitation occurs in the form of discrete, brief thunderstorms (Venter et al. 2003). The park experiences a large latitudinal and seasonal range in minimum and maximum temperatures. For the park as a whole, the mean daily winter temperature is 17.8°C (9.5–26.1°C) while the mean daily summer is 26.4°C (20.4–32.4°C), indicating the mild winters and hot summers experienced. The temperatures have a near-inverse gradient to rainfall where the warmest annual temperatures are recorded in the north-eastern sections of the park and the coolest in the far south-western section (Zambatis 2006).

Eighteen sites were selected for assessment based on the locations of Department of Water and Sanitation (DWS) hydrological flow gauging stations. (**Figure 1, Table 1**). These span five large perennial rivers and nine non-perennial rivers, in seven sub-catchments which traverse the park. Owing to their variable nature the sites cannot be treated as replicates. For the sake of brevity, site names are derived from the first three letters of the river followed by the first letter of the site name (**Figure 1, Table 1**).

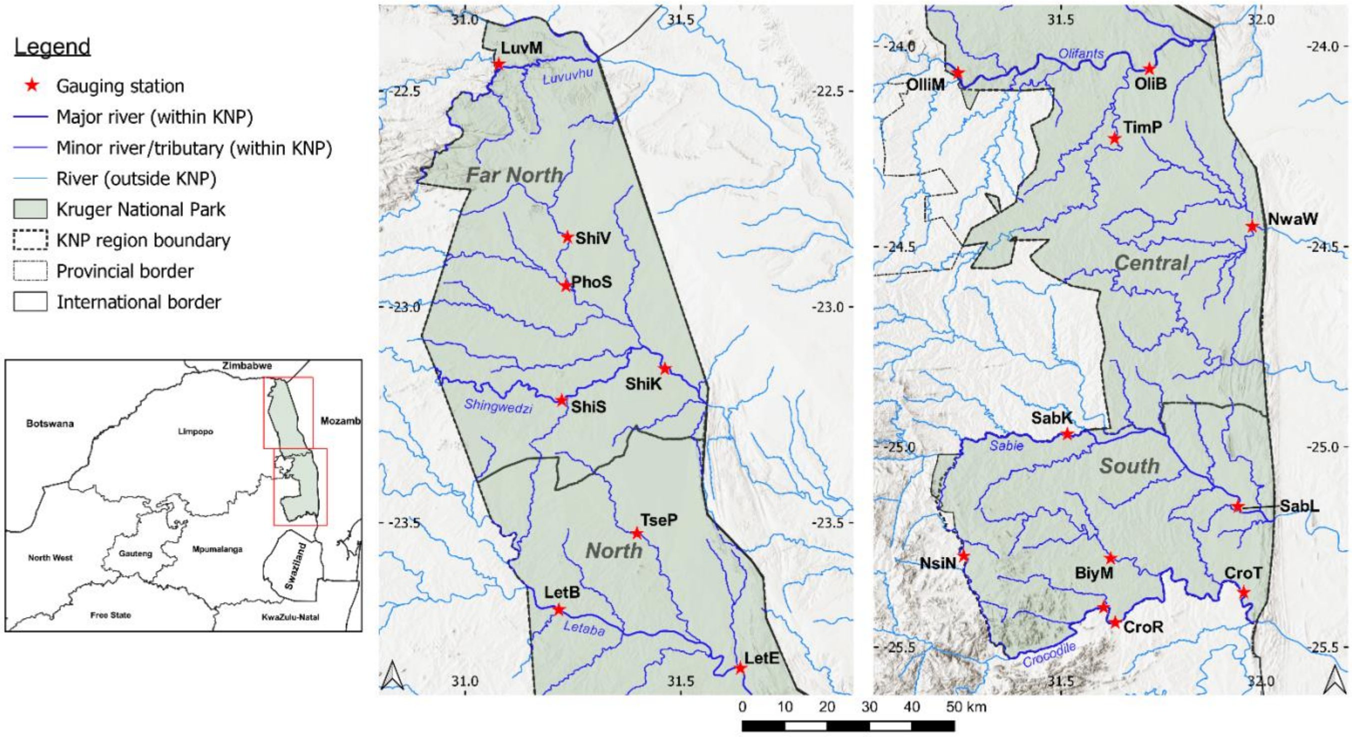


Figure 1. Locations of selected study sites within the Far North and North sections (left panel) and Central and South sections (right panel) of the Kruger National Park. The catchments of BiyM, NwaW and TseP are completely contained within KNP, while the catchments of TimP and ShiV are >90% within KNP or adjacent protected areas. The names of major rivers are indicated.

Riparian woodland cover determination

Gauging station spatial location data were obtained from the DWS (http://www.dwa.gov.za/iwqs/gis_data/). The station vector points were snapped to the nearest river line obtained from the National Geospatial Information (NGI) 2016 topographical vector dataset (www.ngi.gov.za). A circular buffer with a 5 km radius was applied to each point to create a circular polygon to capture areas both up and downstream of the gauging weir. A 300 m buffer was applied to the main river channel lines (on which each point was situated) to incorporate the riparian zones along the river stretches and then clipped to the circular buffer for each site and to the KNP boundary from the South African Protected Areas Database (2018, quarter 2) (Department of Environmental Affairs 2018) to create 18 approx. 10 km long river reach polygons. Finally the difference tool was applied to exclude section ranger homesteads and tourist facilities such as rest camps and picnic sites from the polygons to avoid bias caused by trees which may have been planted or been buffered from flooding or at lower risks from low rainfall since they may be watered artificially. Within each polygon, riparian areas' boundaries were delineated by manually digitising riparian areas from Google Earth (DigitalGlobe/AfriGIS) 2016–2018 Landsat 8 imagery through visual identification of typical dense riparian woodland features and visible soil differences from surrounding savanna, including parts of the river macro-channel to account for possible historical changes in the channel dimensions, and some leeway in the terrestrial component to account for historical change. These new polygon shapefiles (totalling 5 021 ha) were used for analyses.

Riparian woodland extents at selected sites at different times (1936 to 2018) were determined from all available NGI panchromatic (1936–2008) and true colour (2009–2015) historical aerial imagery for the area, supplemented with Landsat 8 imagery (through the QuickMapServices QGIS plugin) (

Table 2) for 2016–2018. Aerial photographs were georeferenced by rubber-stretching images using Thin Plate Spline transformation and nearest neighbour resampling without compression, over existing georeferenced images using recognisable control points. Within each polygon, a number (0.1 × area of polygon (ha)) of random points separated by at least 100 m were generated in QGIS using a point count sampling strategy, resulting in 502 points across all sites. A 5 m buffer was applied to each point to create a 78.5 m^2 circular plot. Each plot was inspected for the presence of any part of an individual distinguishable large tree (through identification of a continuous identifying canopy area typical of riparian trees in the region) and repeated for every available aerial/satellite image of sufficient quality. A binary score was used for absence/presence of an individual tree, based on the visible canopy. Large trees could easily be made out from newer imagery but could not always be differentiated from bush clumps in older photographs, other than sometimes appearing darker and image contrast was asjusted to assist in that regard. The proportion of riparian tree cover was calculated from the plots within each polygon. In some instances, older aerial imagery did not fully cover the riparian polygon/s and in these cases, years with less than a third of each site's total points were removed to avoid skewed data for a particular year. Imagery date was used where given, however, if the day of imagery was not available, the first day of the month was used. If only the year was available, the date assigned to an image was 1 January. All geospatial functions were conducted in QGIS (QGIS Development Team 2018).

Environmental data

Streamflow/discharge records in the form of daily average flow (DAF) and monthly flood peak (MFP) data were extracted from the DWS Hydrological Services verified data repository for each of the selected gauging stations/sites (Department of Water & Sanitation 2018). Gauging stations became operational and were decommissioned or damaged (and not repaired) at different times and thus periods of data availability vary between sites (**Table 1**). Only sites with data reliability (a metric determined by DWS as a measure of data accuracy based on various factors) of 75% or more were used for streamflow analyses. For each site, rainfall data from the closest weather station were acquired from the South African Weather Service (SAWS). The time periods available differed between weather stations (**Table 3**).

Table 1. DWS Hydrological gauging station/study site details.

Gauging station number	Gauging station name	River	Sub-catchment	Site code used in the study	Coordinates		River flow record period availability (at time of data download)	Data reliability (%)	River flow[a]
					Latitude	Longitude			
A9H013	Mutale River	Mutale & Luvuvhu[†]	Limpopo	LuvM	-22.437734	31.077833	1988/12/01–2018/01/31	81	Non-perennial[§]
B9H001	Vlakteplaas	Shisha	Shingwedzi	ShiV	-22.838542	31.237093	1960/09/01–P	92	Non-perennial
B9H004	Sirheni Dam	Mphongolo	Shingwedzi	PhoS	-22.950967	31.233744	1983/11/01–2013/01/31	93	Non-perennial
B9H003	Silvervis	Shingwedzi	Shingwedzi	ShiS	-23.143270	31.462620	1984/10/30–2013/02/07	99	Non-perennial[§]
B9H002	Kanniedood	Shingwedzi	Shingwedzi	ShiK	-23.215280	31.220000	1984/02/01–2013/01/20	100	Non-perennial[§]
B8H019	Pioneer Dam	Tsendze	Letaba	TseP	-23.526221	31.397727	1984/02/01–2018/01/31	98	Non-perennial
B8H034	Black Heron Dam	Letaba	Letaba	LetB	-23.702173	31.216620	1988/10/01–2018/02/28	75	Non-perennial[§]
B8H018	Engelhardt Dam	Letaba	Letaba	LetE	-23.838610	31.640830	1984/03/01–2017/02/28	86	Non-perennial[§]
B7H026	Balule	Olifants	Olifants	OliB	-24.056525	31.720919	1994/08/01–P	28[‡]	Perennial
B7H015	Mamba	Olifants	Olifants	OliM	-24.066280	31.242880	1987/11/01–2018/03/31	92	Perennial
B7H020	Piet Grobler Dam	Timbavati	Olifants	TimP	-24.231000	31.634000	1988/11/01–2018/04/30	90	Non-perennial
X4H004	Wenela Drift	N’wanetsi	N’wanetsi	NwaW	-24.449722	31.976944	1960/12/01–2018/04/30	81	Non-perennial
X3H021	Kruger Gate	Sabie	Sabie	SabK	-24.968472	31.515417	1990/12/01–2018/04/30	93	Perennial
X3H015	Lower Sabie Rest Camp	Sabie	Sabie	SabL	-25.149528	31.940667	1987/01/01–P	92	Perennial
X2H072	Nsikazi River	Nsikazi	Crocodile	NsiN	-25.272277	31.256181	1990/01/01–2018/04/30	77	Non-perennial
X2H018	Mbyamiti Weir	Biyamiti	Crocodile	BiyM	-25.278388	31.622581	1960/10/01–1997/02/28	90	Non-perennial
X2H016	Tenbosch	Crocodile	Crocodile	CroT	-25.363861	31.955722	1960/10/17–2018/04/13	93	Perennial
X2H046*	Riverside	Crocodile	Crocodile	CroR	-25.398889	31.610556	1985/10/30–P	99	Perennial
X2H017*	Thankerton van Graan	Crocodile	Crocodile	CroR	-25.438377	31.634525	1959/09/01–1998/08/03	84	Perennial

[a] Classifications vary depending on literature. See O’Keefe & Rogers 2003; Rossouw et al. 2005; Pollard et al. 2011.

[†] The A9H013 station is located near the confluence of the Mutale and Luvuvhu Rivers and the study comprised mostly riparian sections along the latter.

[§] Historically perennial, now seasonal.

[‡] Insufficient reliable flow data available for analysis. The station and was retained as a site for tree cover and rainfall analyses but not analysis of flow parameters.

* X2H046 and X2017 were amalgamated into one site (due to their close proximity) and the midpoint between the two gauging stations was used to delineate the site polygon for analysis.

P = date of data download (2018/06/01).

Table 2. Image dates of aerial photographs (1936–2015) and Landsat 8 satellite imagery (2016–2018) used in the study for each site. Where exact dates are not available, year or year and month are provided. All imagery prior to 2004 was black and white and thereafter colour.

Study site	**Dates of aerial photographs/satellite imagery**								
	1930–1939	**1940–1949**	**1950–1959**	**1960–1969**	**1970–1979**	**1980–1989**	**1990–1999**	**2000–2009**	**2010–2018**
LuvM		1942/08*		1962/10/03	1970/07/28 1977/08/28	1987/06/25	1995/06/22	2004/07/26 2008	2012 2015 2017/04/06
ShiV		1942/08*		1963/03/27	1971/08/17 1977/07/28*	1987/06/17	1999/05/04	2004/07/24 2008	2012 2015 2017/10/19
PhoS		1942/08*			1971/08/16 1977/09/18	1987/06/24	1999/05/04*	2004/07/24 2008	2012 2015 2017/10/19
ShiS				1963/03/27	1971/08/06 1977/07/19	1989/08/24		2001/06/17 2004/07/24 2008	2012 2015 2017/10/19
ShiK				1963/03/27	1971/08/06 1977/10/13*	1989/08/12		2001/06/17 2004/07/24 2008	2012 2015 2018/08/25
TseP				1963/03/22 1965/09	1977/06/03	1989/07/24		2001/06/16 2004/07/24 2009	2012 2015 2018/09/06
LetB			1954/06	1960/05/04 1965/09	1972/08/04 1977/07/20	1989/08/12		2001/06/16 2004/07/24 2009	2012 2015 2018/09/10
LetE				1965/09	1972/08/24	1989/07/31		2001/06/16 2004/07/24 2009	2012 2015 2016/06/26
OliB		1944		1965/09	1974/06/16 1977/07/20	1986/06/02	1994*	2009	2012 2015 2016/02/03
OliM		1944	1954/06	1960/05/04 1965/09	1974/06/16	1986/05/30	1997/08/10	2002/07 2008	2012 2015 2018/09/06
TimP		1944		1965/09	1974/06/20	1986/06/02	1997/08/10	2009	2012 2015 2016/03/02
NwaW				1965/10	1974/06/20	1986/06/05	1997/08/12*	2009	2012 2015 2016/07/21
SabK				1965/10	1974/06/22	1984/07	1996/05/24	2002/07	2012

							1997/09/28	2009	2015 2018/07/30
SabL		1940		1965/10	1977/04/15	1985/07/06	1997/09/28		2010 2012 2015 2016/07/14 2017/12/03
NsiN	1936	1940*	1954/06 1959/08/23	1965/10	1970/06/05	1984/06/30	1995/06/09 1996/04/25 1997/09/28*	2003/08/16	2010 2012 2015 2018/07/21
BiyM		1940	1959/08/27	1963 1965/10	1977/04/15	1984/06/30*	1997/09/28	2003/08/17	2010 2012 2015 2018/08/21
CroT	1939			1963/06/27* 1965/10	1977/04/20 1979/08/06	1984/07/03 1985/07/06	1997/09/28	2003/08/17	2010 2012 2015 2017/04/27
CroR	1939		1959/08/23	1963* 1965/10	1977/04/20 1979/08/06	1984/07/03 1988/05/30	1997/09/28	2003/08/16	2010 2012 2015 2018/08/21

* Imagery from the particular year was of insufficient quality, scale or coverage for analysis.

Table 3. Weather station information and time-span of data available at the time of data collection.

Station number	Station name	Sites applicable	Coordinates		Rainfall data period	Duration (years)
			Latitude	Longitude		
0812567A8	Teba Pafuri	LuvM	-22.450	31.320	1981/05/01–P	37
0768382 0	Shingwedzi/Vlakteplaas	ShiV PhoS	-22.867	31.217	1983/04/01–P	35
0725373 X	Letaba/Woodlands	ShiS ShiK	-23.217	31.217	1983/01/14–P	35
0681691 9	Letaba/Mooiplaas	TseP	-23.517	31.400	1976/01/01–P	42
0681249 4	Letaba/Mahlangeni	LetB	-23.650	31.150	1986/10/01–P	32
0639391 X	Olifantskamp	LetE	-24.017	31.733	1974/01/01–P	44
0639274 2	Houtboschrand	OliB TimP	-24.067	31.667	1982/10/01–P	36
0638579 X	Ingwelala	OliM	-24.150	31.333	1976/03/01–P	42
0596063 7	Talamati	NwaW	-24.550	31.550	1991/07/01–2010/12/26	19
0596179 3	Skukuza	SabK	-24.980	31.600	1911/09/01–P	107
0556679 8	Stolznek	NsiN	-25.317	31.383	1982/11/01–P	36
0557379 X	Mbyamiti	BiyM	-25.317	31.717	1991/11/01–P	27
0557712 6	Krokodilbrug	CroT SabL	-25.367	31.900	1938/11/01–P	80
0556898 7	Malelane	CroR	-25.467	31.500	1983/11/01–P	35

P = date of data download (2018/12/19).

Data and statistical analyses

Data and statistical analyses were conducted in R (R Core Team 2017) using the *tidyvers*e (Wickham 2017), *lubridate* (Grolemund & Wickham 2011), dplyr (Wickham et al. 2018), *MASS* (Venables & Ripley 2002), *ggplot2* (Wickham 2009) and *ggpubr* (Kassambara 2018) libraries. In addition to using the raw flow and rainfall data, these were also converted to regular time-series data structures (in months) and a deseasonalised (low-frequency variation trend) dataset was created from the raw data using the *stlplus* library (Hafen 2016) to reveal longer-term trends and maintain the effect of peak events in the data by adjusting or smoothing seasonal variations (Cleveland et al. 1990; Dokumentov et al. 2015). The trend data was smoothed using LOESS (locally-weighted scatterplot smoothing) regression. Due to local variable characteristics of the sites throughout the park, each one's specific trends were derived individually.

Overall change (difference in tree cover) was obtained by calculating the slope between the first and last tree cover value at each site for the entire period. Mean annual change in tree cover at each site was compared to the site's median tree cover and a Spearman's correlation test was used to assess if there were significant relationships between them. Mann-Kendall (non-parametric) tests, using the *Kendall* library (McLeod 2011), were run to statistically assess for monotonic trends over the period. Additional aspects of the raw data were derived to assess whether these had some influence on tree cover (**Table 4**). These variables were used for one-way ANOVA, followed by post-hoc Tukey HSD tests where necessary, to assess if there were significant differences in tree cover and tree cover change, rainfall and flow variables between sites, regions, geology, flow perenniality and river orders. Levene's test, using the *car* library (Fox & Weisberg 2011), was used to assess the homogeneity of variances in the explanatory variables. Where this test was failed a Welch one-way ANOVA or Kruskal-Wallis test was used.

Multiple linear regression was used to determine if any of the variables explained changes in tree cover. This was done for data for the sites combined (i.e. KNP as a whole) as there were not enough data points per site to assess within sites. One extreme outlier was removed from the dataset as it resulted in over-dispersion and thus had an adverse effect on the linear model. An Akaike's Information Criterion (AIC) stepwise model selection algorithm was used to determine the best-fit model from the list of variables. This was followed by a mixed effects model with random effects using the *nlme* library (Pinheiro et al. 2018). Although R-squared values aren't obtained in a standard mixed effects model, a pseudo R-squared value was obtained by using the *MuMIn* package (Barton 2018).

Table 4. Variables created from raw data for analysis and used in ANOVAs and multiple linear regression model.

Data category	Variable	Description
Site Characteristics	site	code for site name (see Table 1)
	region	KNP region†
	perenn	Perennial/Non-perennial‡
	order	Strahler's Stream Order
	geology	Primary underlying simplified geology – basalt or granite.
	veg_p_change	Proportional change in tree cover from last recorded tree cover standardised to annual rate
Flow	avedayflow	Mean daily flow (m^3/day) (based on mean flow per day × 3600 × 24) during the time period between each successive aerial image per site.
	cltvflow	Total/cumulative flow during the time period between each successive aerial image per site.
	maxpeak	Maximum flow record during the time period between each successive aerial image per site.
	flowCV	Coefficient of variation of flow during the time period between each successive aerial image per site.
	flood	Number of high flow events (>10× mean flow) per year during the time period between each successive aerial image per site.
	Drought	Number of low flow events (<0.1 × mean flow) per year during the time period between each successive aerial image per site.
Rainfall	meanrain	Mean monthly rainfall during the time period between each successive aerial image per site.
	cltvrain	Total/cumulative precipitation during the time period between each successive aerial image per site.
	maxrain	Maximum monthly (calendar) rainfall recorded during the time period between each successive aerial image per site.
	rainCV	Coefficient of variation of rainfall during the time period between each successive aerial image per site.
	meanwinrain	mean winter (June, July & August) rainfall
	meansumrain	Mean summer (December, January & February) rainfall during the time period between each successive aerial image per site.

† Olifants River is the border of central and north regions. Olifants River sites were classified as central in this study.
‡ Based on the most current literature, not historical flow characteristics.

Results

Tree cover change

All eighteen sites experienced fluxes in tree cover over the course of the period analysed (**Figure 2**). Median tree cover during the period was statistically different between sites using a Kruskal-Wallis test ($\chi^2(17) = 134.3$, $P < 0.001$). Across the whole park, there were no statistically significant differences in proportional tree cover change per annum within each time period between sites ($F_{(16, 132)} = 0.376$, $P = 0.986$), regions ($F_{(3,146)} = 0.818$, $P < 0.486$), non-perennial and perennial rivers ($F_{(1,148)} = 0.189$, $P = 0.664$), stream orders ($F_{(4,145)} = 0.19$, $P = 0.943$) or underlying geology ($F_{(1,148)} = 0.86$, $P = 0.77$), as determined by one-way ANOVA tests. In terms of overall change of tree cover in the period (range = -0.59%–0.23% Δ), tree cover increased at six sites and decreased at eleven sites, with one site (CroT) showing no change (**Figure 2, Figure** 3). Of those sites that experienced an increase, only one (OliM) was on a perennial river. The LOESS curves revealed minimal fluctuation in tree cover at both Let, both Oli sites, and at SabL . Several sites (BiyM, CroR, NsiN, PhoS, SabK, SabL and ShiK) showed a pattern of increasing tree cover towards the middle of the study period (1960s–1990s). In terms of the trend in tree cover, rather than overall change, three sites (NwaW, TimP and TseP) increased (only TseP was significant), while there is a decreasing trends at 14 sites, six of them had a statistically significant downward trend (LuvM, NsiN, OliB, PhoS, SabK, SabL and ShiS). Another trend is that of decreasing tree cover from the 1990s onwards at most of the sites (**Figure 2**). The highest tree cover during the study period, being 79%, was recorded at SabK in 1996. Other sites with high tree cover (>40%) at some point were LuvM, the Shingwedzi River sites, ShiV, NwaW and NsiN. There was low tree cover (<0.15%) at both Crocodile River sites, both Letaba River sites, both Olifants River sites, SabL and TimP.

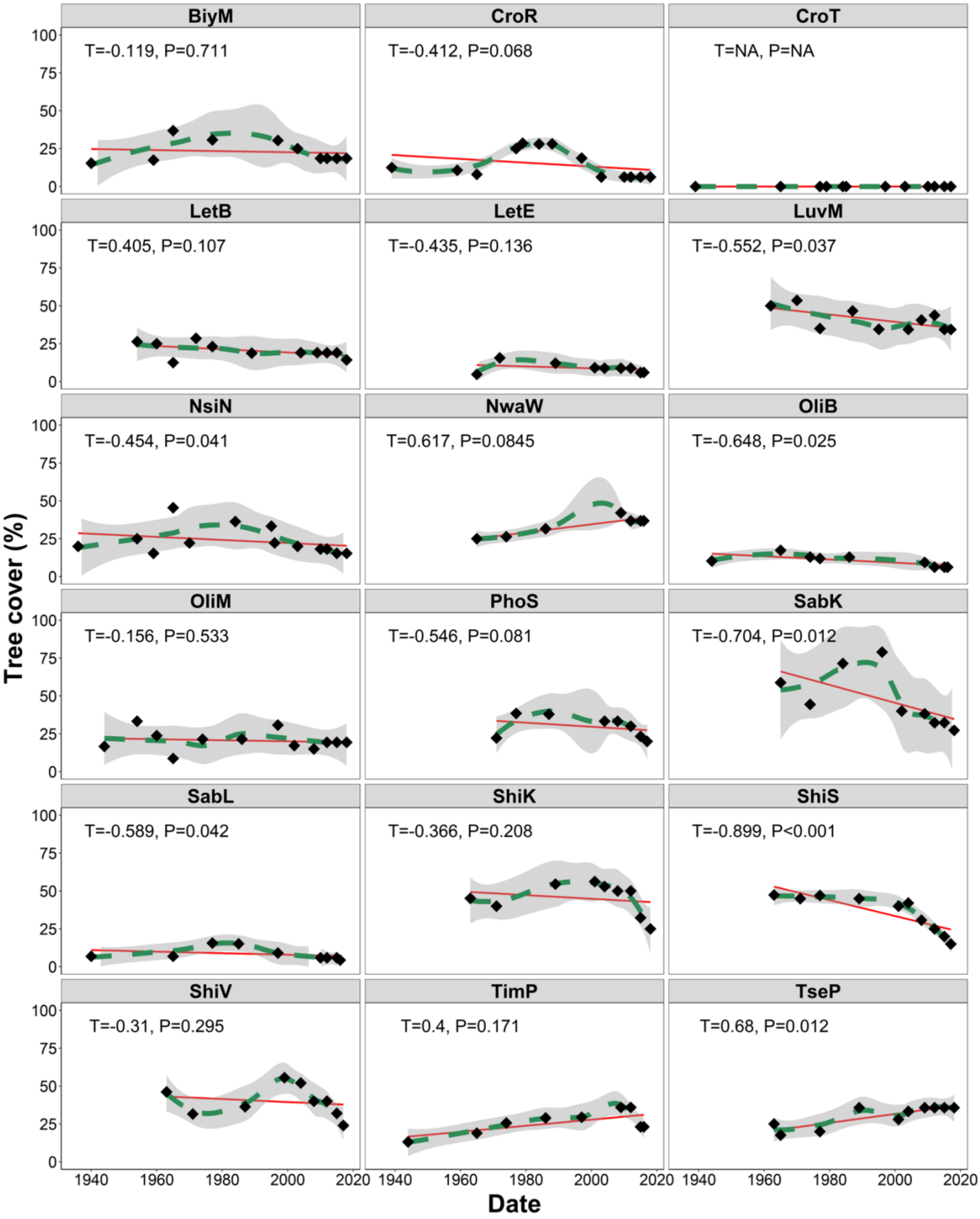


Figure 2. Tree cover change trends at each of the study sites. Points represent the measured tree cover percentage at a given time. A LOESS curve with a 95% confidence band was fitted (green line with grey band) to detect the smoothed trend over time, while linear regression line was fitted (red line) to the data simply to visually display the overall trend at each site. The Mann-Kendall tau coefficients for monotypic trend (+ = upward, - = downward) and P-values at the 95% confidence interval are given.

There was a moderate negative correlation between the mean tree cover change per year and median tree cover during the study period ($r_S = -0.441$, $p = 0.067$) (**Figure 3**Error! Reference source not found.). Sites with higher tree cover generally tended to lose more per year, with SabK and ShiS experiencing the greatest mean annual loss. That said, the three sites (TimP, TseP, NwaW) that experienced the greatest overall gains in tree cover all had a median tree cover of >20% for the study period.

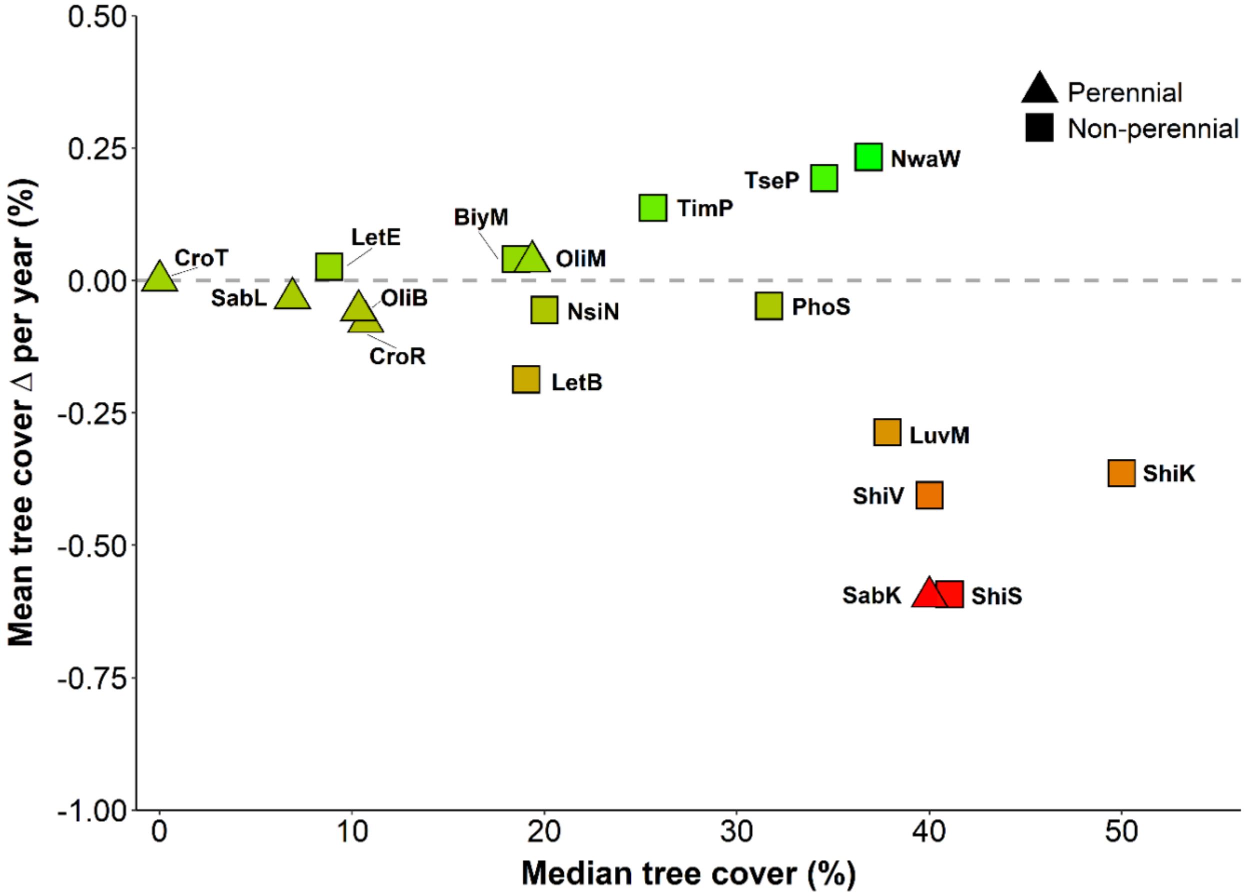


Figure 3. Change in tree cover per year versus the median tree cover percentage during the study period, for each site. Colours are graded red to green by mean tree cover change per year.

Hydrological changes

Six of the sites (BiyM, CroR, CroT, PhoS, ShiK and TimP) show a decreasing *trend* in mean monthly flow over the period investigated, of which two were statistically significant (CroT and TimP) (**Figure 4**). The remainder of the sites all show an increasing trend in mean monthly flow of which six had a statistically significant upward trend (LetB, LetE, NsiN, SabK, SabL and ShiV). There is little to suggest that flood events are becoming bigger from the flow records, however, the hydrographs and **Figure 7** indicate more regularly occurring high-flow events at NsiN, OliM, SabK and ShiV. OliB was omitted from analysis due to the low number of flow records available.

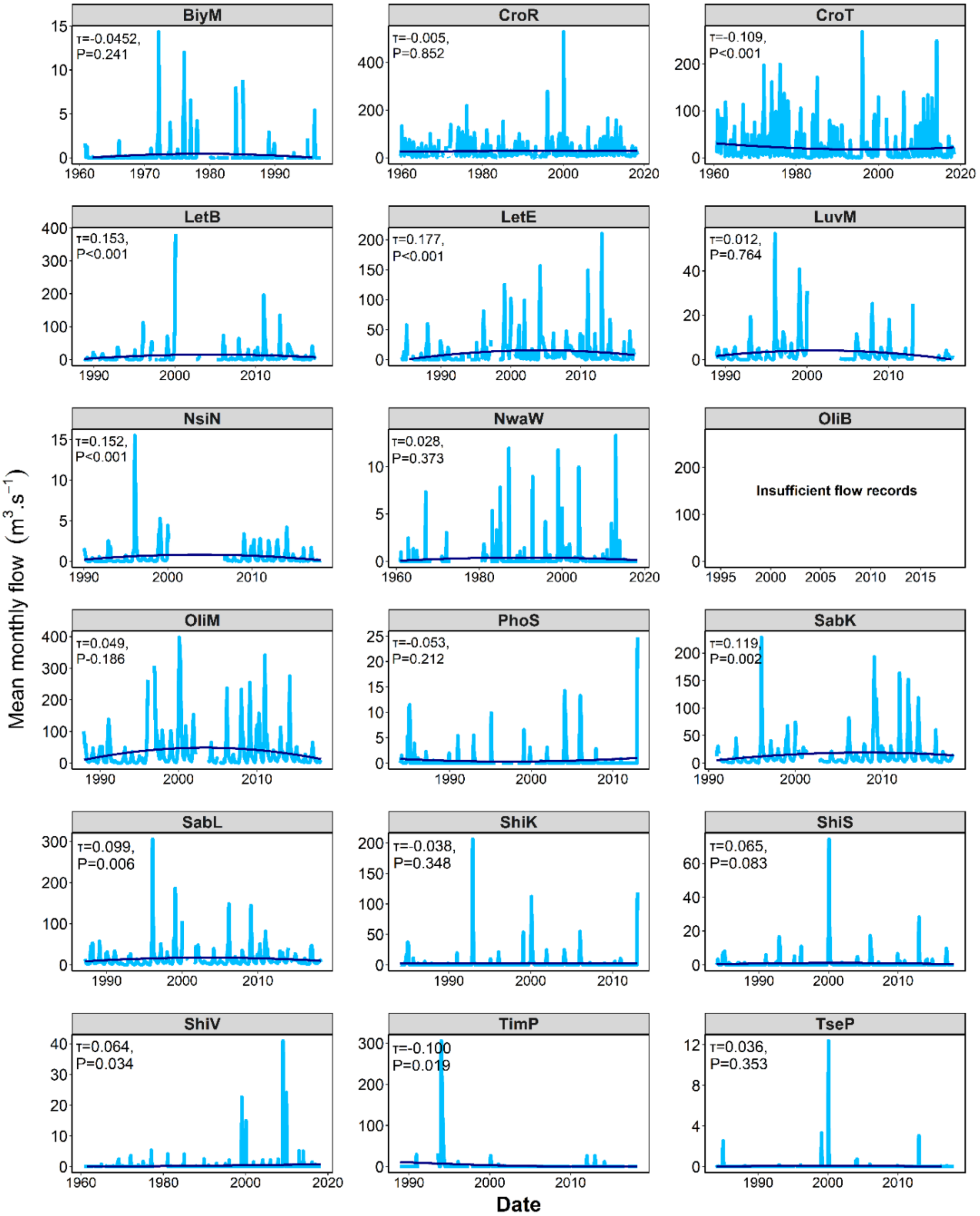


Figure 4. Flood hydrographs of mean monthly flow for each study site. A LOESS regression line (dark blue) was fitted to visibly depict the overall trend in flow, considering the continuous nature of the data. The Mann-Kendall tau coefficients for monotypic trend (+ = upward, - = downward) and P-values at the 95% confidence interval are given. Site OliB did not have sufficient flow records for meaningful analysis.

Spatio-temporal trends in flow, rainfall and tree cover

The trends of tree cover, deseasonalised river flow and rainfall were spatio-temporally variable (**Figure 5**Error! Reference source not found.). Some of the sites show no consistent relationships. For example, the rainfall and resultant flood event of 2000 seemed to have had little effect on tree cover at the Letaba sites (LetB and LetE); however, a decrease in rainfall between 2005 and 2010 preceded a decline in tree cover. At LuvM, high flow ca. 2000 appear to have spurred an increase in tree cover, but the opposite is true ca. 2014 when subsequent high flow events occurred. High rainfall ca. 2009 appears to precede a small decrease in tree cover at NwaW. Tree cover loss appears to have followed the 2000 floods at OliM, where the highest vegetation cover since 1950 was recorded just prior to floods (**Figure 2**), after a period of lower rainfall and decreased flow. Tree cover appears to decrease ca. 2000 at TseP, SabK, ShiK, ShiS and ShiV. TimP, TseP, LuvM and OliM experienced what appears to be a recovery in tree cover after ca. 2000. Although there is a consistent pattern of decrease in tree cover from ca. 2000, the rate of decline seems to accelerate particularly ca. 2010, although some sites experienced earlier declines (i.e. SabL, NsiN and LuvM) (**Figure 2,Figure** 5).

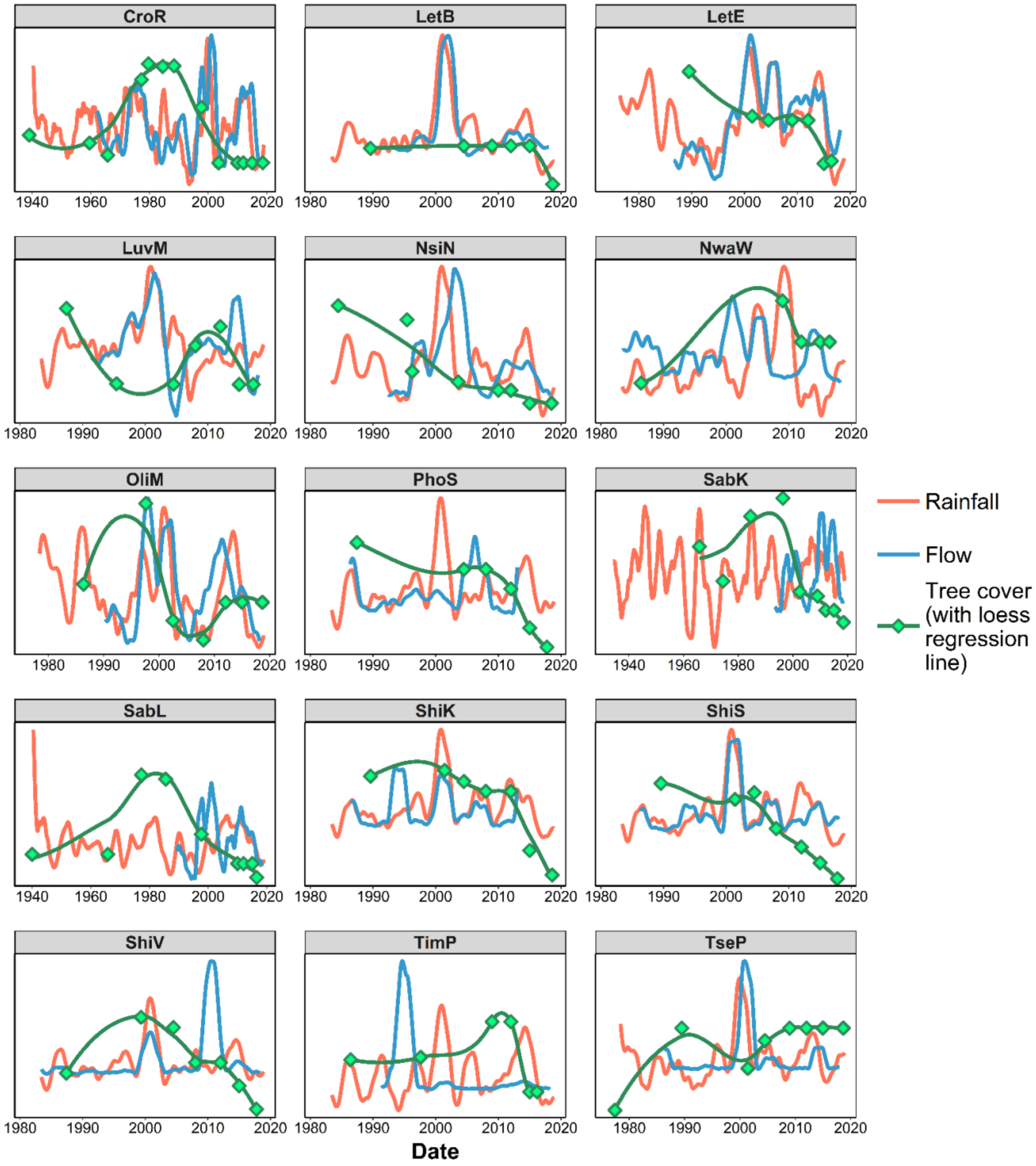


Figure 5. Trends in tree cover, deseasonalised rainfall and deseasonalised river flow at each study site. Smooth moving average lines were used for rainfall and flow. A LOESS regression curve was fitted to tree cover data to show trends at each site. Three sites excluded were OliB for the low flow data availability and reliability, CroT due to the zero values for tree cover and BiyM due to the minimal overlap of the three variables. Data was scaled to ensure fit on one graph and thus scale does not represent actual values.

Where there was an overlap of flow records and tree cover, various aspects of flow were plotted against *proportional* tree cover change in each period (between successive available aerial images) (

Figure 6Error! Reference source not found.). There were no consistent trends for mean daily flow nor flow CV with tree cover responding differently across time and spatially. For cumulative flow; relatively low values always corresponded with an increase in tree cover at OliM, and a decrease in tree cover at ShiS. Relatively high cumulative flow was associated with either increases or no change in tree cover at NwaW, ShiK and ShiV. Relatively high peak flow events always coincided with tree cover gain at ShiK and NwaW. Conversely, relatively low peak flow events coincided with a decrease in tree cover at SabL, SabK, PhoS, OliM and LetB. An increase in tree cover associated with low peak flow events was evident at BiyM.

In terms of extreme values; very high cumulative flow values appear to be associated with increases in tree cover at CroR, NwaW and SabK, and decreases at SabL, ShiS and TseP. An increase in tree cover at BiyM and decreases at both Sabie River sites seem to coincide with very low cumulative flow figures. Very high maximum peak flow records occurred in time periods when tree cover decreased at CroR, LetE, LuvM, SabK, PhoS, ShiS, TimP and TseP. Very low maximum peak flow values coincided with a decrease in tree cover at PhoS, ShiK and LetB, while an increase in tree cover occurred only at BiyM. High flow CV values corresponded with decreases in tree cover at LuvM, ShiK, PhoS and ShiS. At CroR, LetE and SabL the highest flow CV values were recorded in the same period as the biggest losses in tree cover at each site.

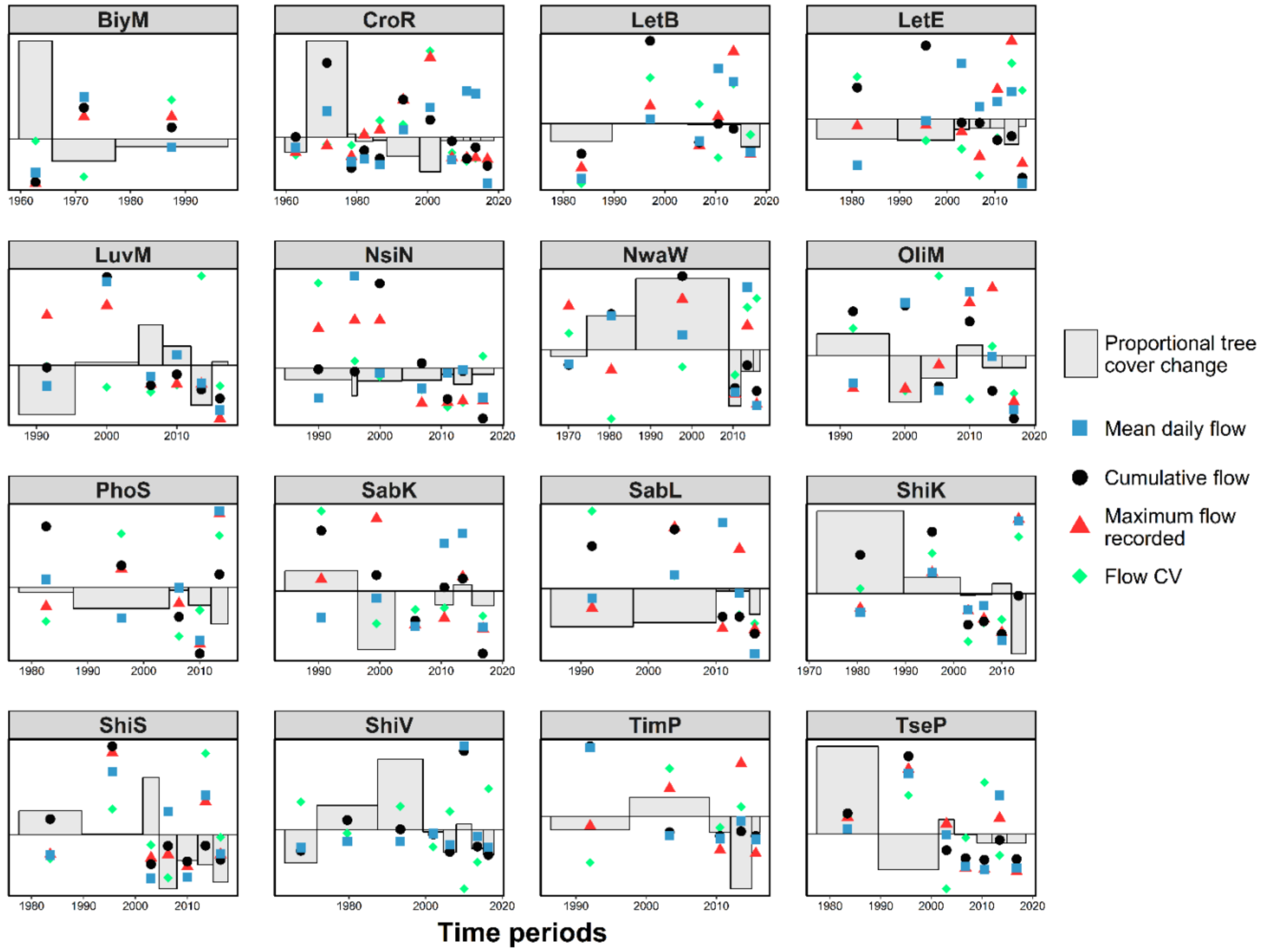


Figure 6. River flow (mm) characteristics for each time period (of overlapping data) and proportional tree cover change at the end of each time period between successive aerial images. All data was scaled to ensure that all variables could be plotted on the same axis . Tree cover bars above the horizontal line indicate periods in which tree cover increased from the previous extent, while those below the line indicate decreases in tree cover from the previous extent. Bar width is relative to the length of each period. Points above the horizontal line indicate values above the mean value, while those below the horizontal line are values below the mean value for the variable. Two sites were omitted from the facet plot namely; OliB for the low flow data availability and reliability and CroT due to the zero values for tree cover. Maximum flow values for ShiV were considered erroneous.

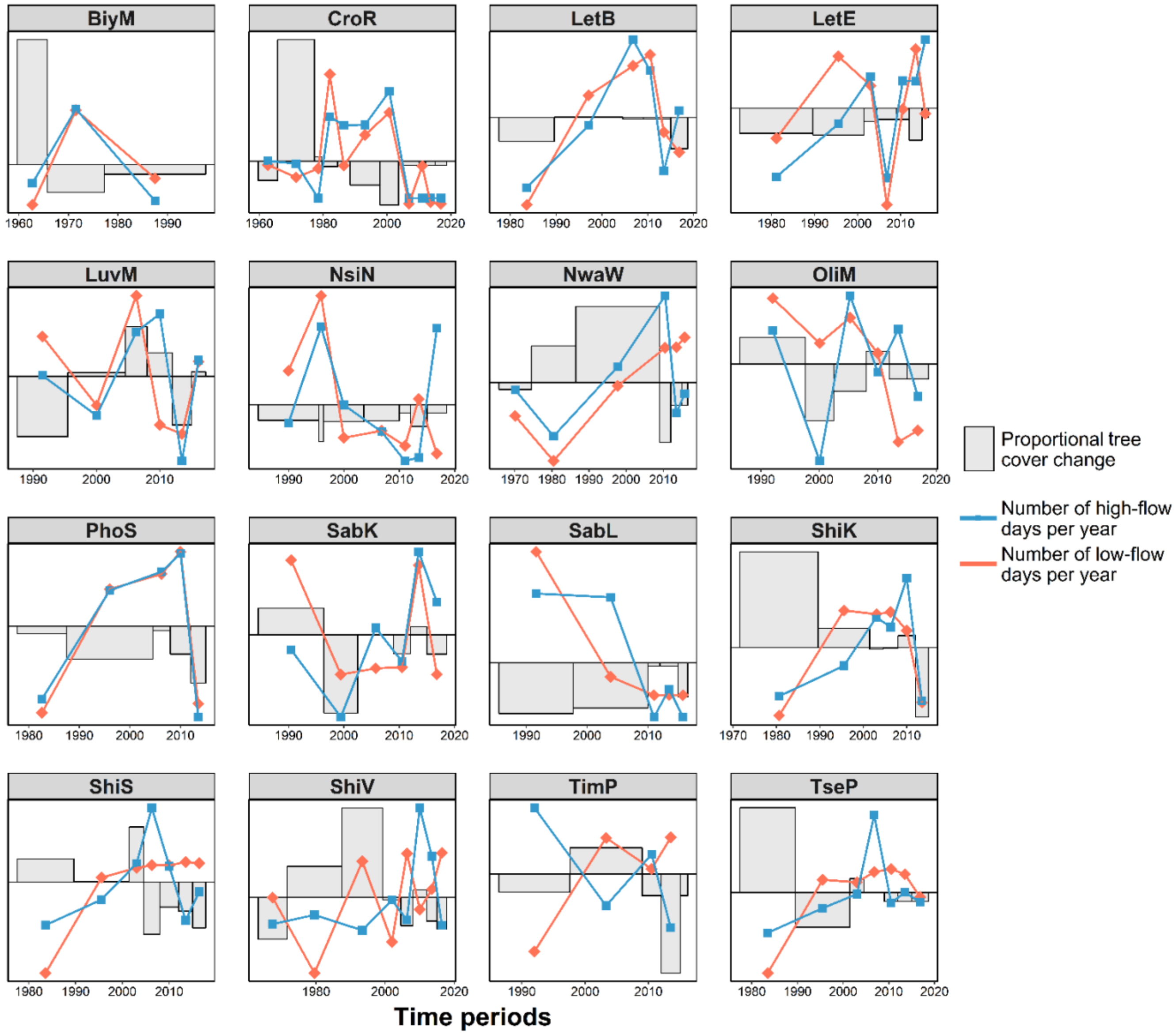


Figure 7. Number of high-flow (10 × daily average flow) and low-flow (0.1 × daily average flow) events per year during each time period relative to proportional tree cover change at the end of each time period between successive aerial images. All data was scaled to ensure that all variables could be plotted on the same axis. Tree cover bars above the horizontal line indicate periods in which tree cover increased from the previous extent, while those below the line indicate decreases in tree cover from the previous extent. Bar width is relative to the length of each period. Points above the horizontal line indicate values above the mean value, while those below the horizontal line are values below the mean value for the variable. Two sites were omitted from the facet plot namely; OliB for the low flow data availability and reliability and CroT due to the zero values for tree cover.

Where there was an overlap of flow records and tree cover, various aspects of flow were plotted against *proportional* tree cover change in each period (between successive available aerial images) (Figure 8

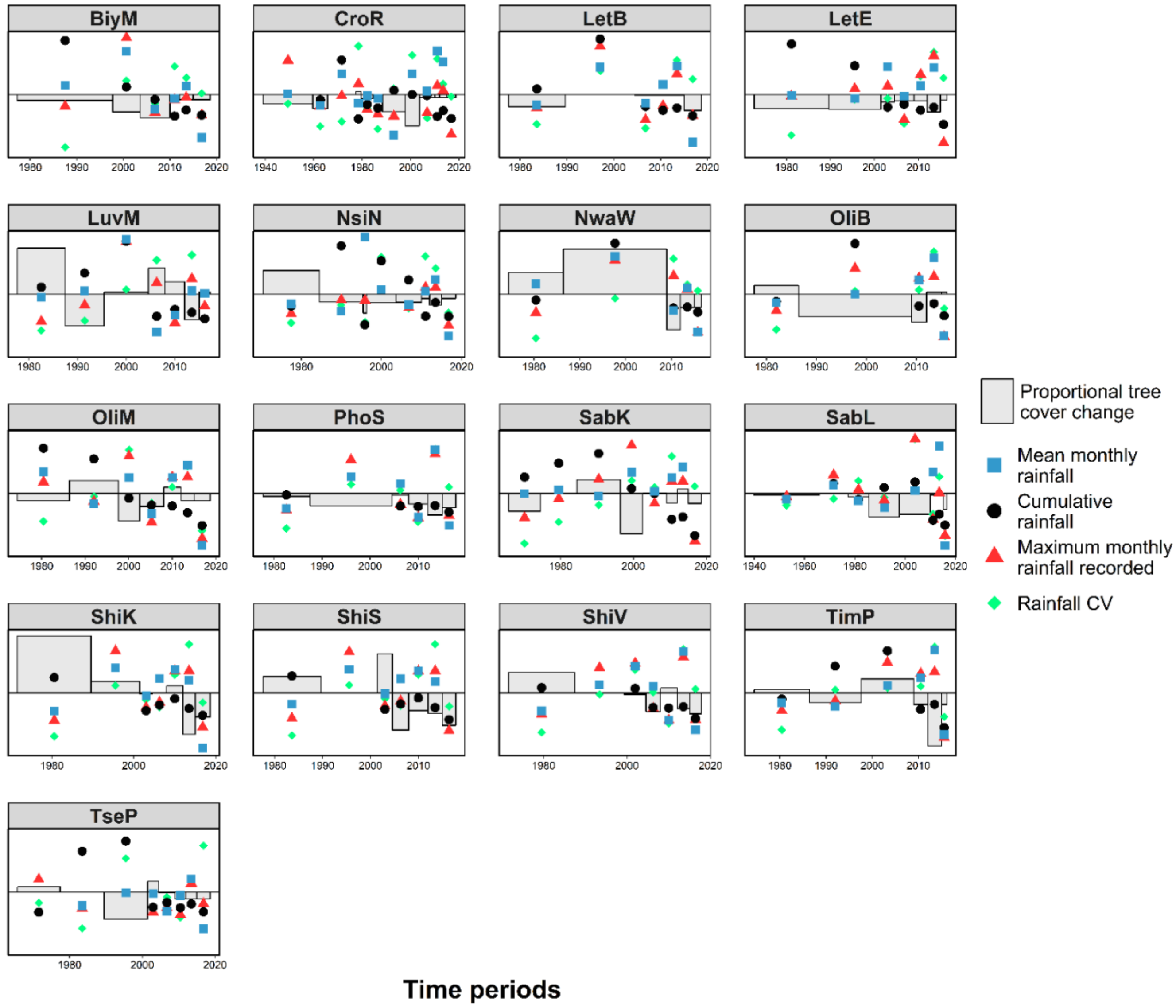


Figure 8. Rainfall characteristics for each time period (of overlapping data) and proportional tree cover change at the end of each time period between successive aerial images. All data was scaled to ensure that all variables could be plotted on the same axis. Tree cover bars above the horizontal line indicate periods in which tree cover increased from the previous extent, while those below the line indicate decreases in tree cover from the previous extent. Bar width is relative to the length of each period. Points above the horizontal line indicate values above the mean value, while those below the horizontal line are values below the mean value for the variable.

). Relatively high mean rainfall within each period was synonymous with an increase in tree cover at NwaN and a decrease at ShiS. Relatively low mean rainfall always occurred simultaneously with a decrease in tree cover at LetB. While there was no direct association with relatively low cumulative rainfall, relatively high values were always associated with an increase in tree cover at TimP and decreases at ShiV, ShiK, PhoS and BiyM. There were no trends consistent with maximum monthly rainfall. Lower than average rainfall CV only coincided in every time period at NwaW.

Extreme high mean monthly rainfall values within each site corresponded with increased tree cover at NwaW and decreased tree cover at NsiN and TimP. Very low mean monthly rainfall coincided with increased tree cover at LuvM and a decrease in tree cover at LetB and ShiK. Extreme high cumulative rainfall in the time periods coincided with increased tree cover at TimP and NwaW, while tree cover decreased at TseP and OliB. While below-average maximum monthly rainfall figures did not correspond directly to tree cover at any site, above-average figures corresponded with increased tree cover at NwaW and decreased tree cover at OliM, PhoS, BiyM and a very substantial decrease SabK.

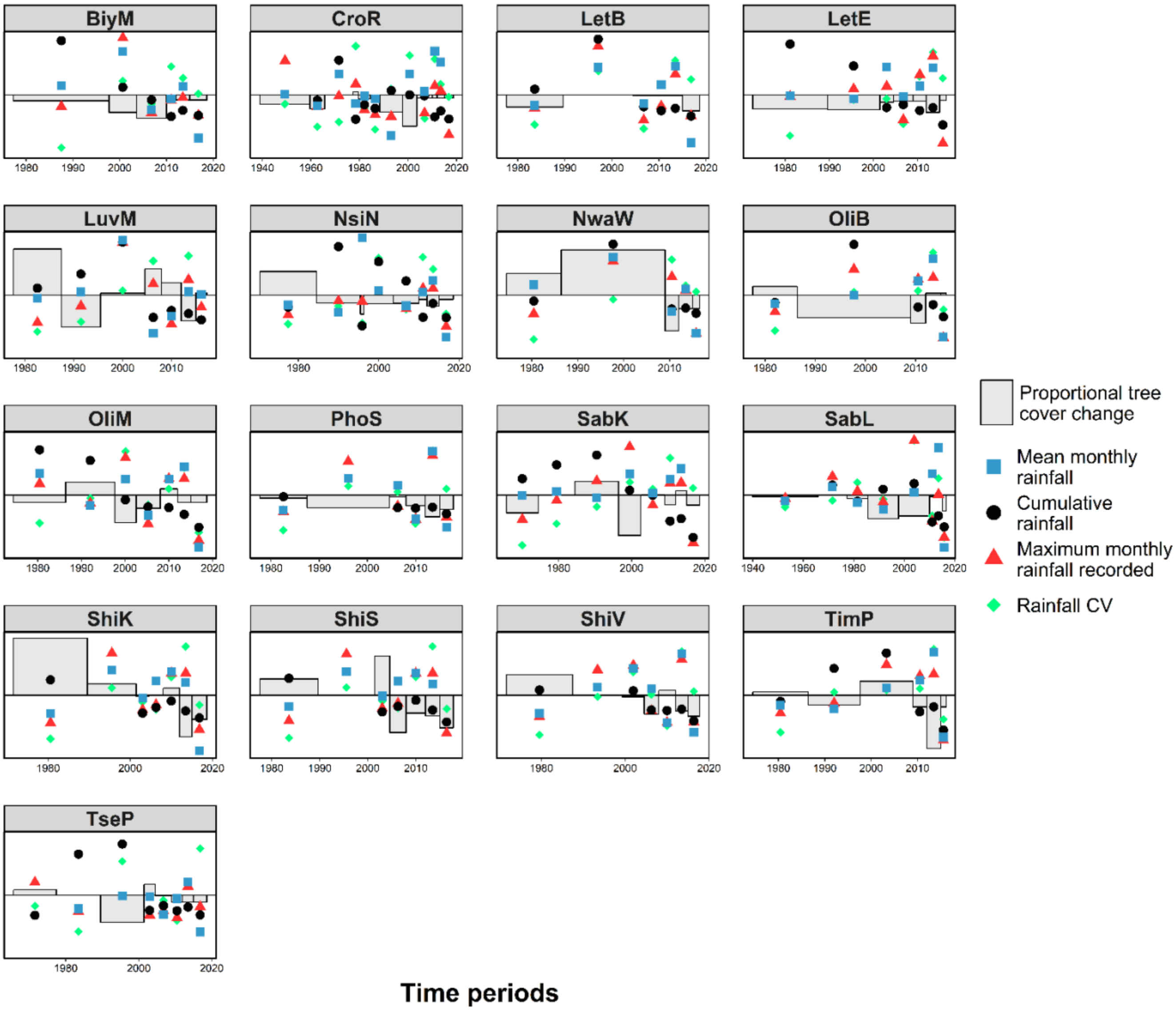
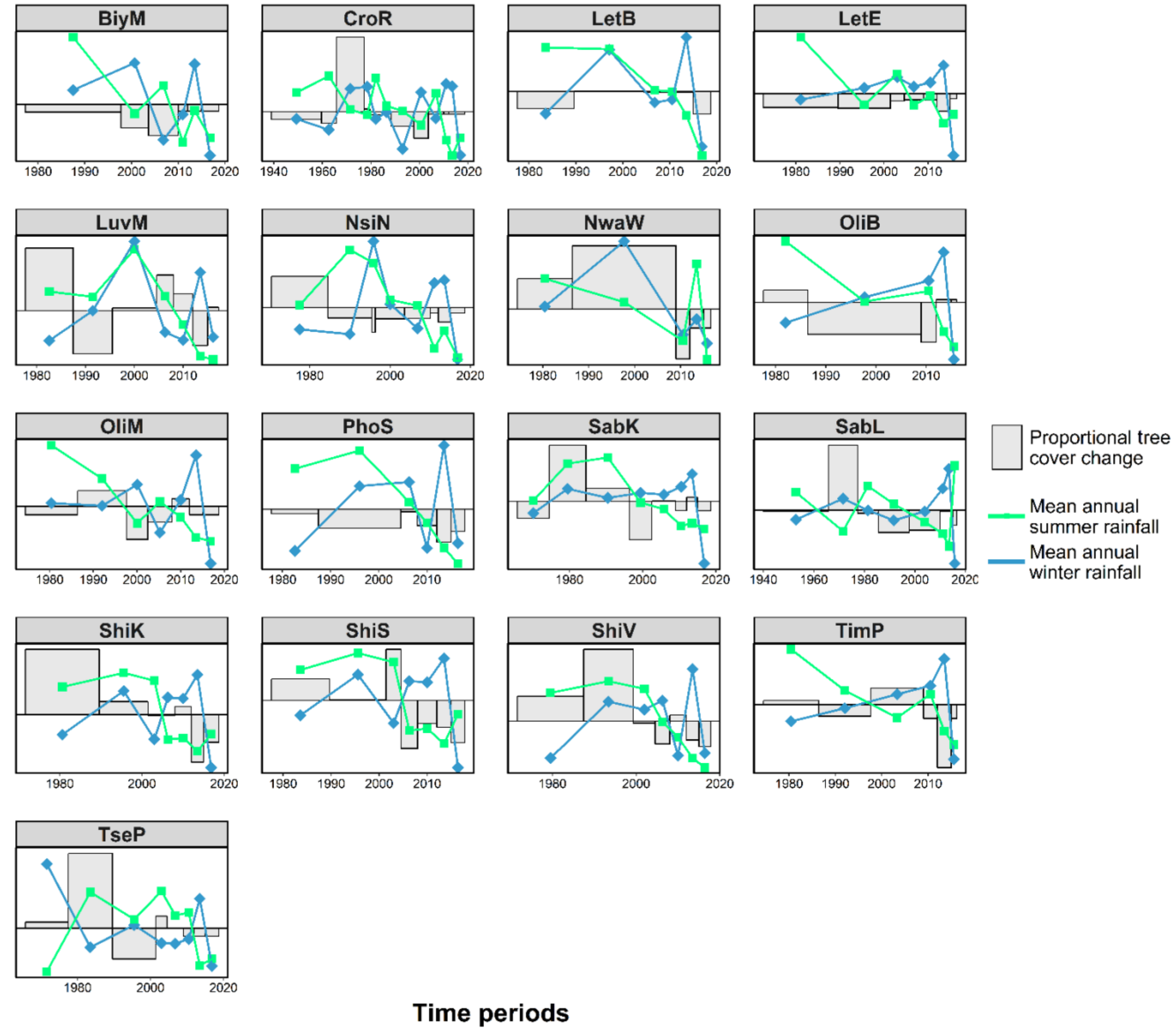


Figure 8. Rainfall characteristics for each time period (of overlapping data) and proportional tree cover change at the end of each time period between successive aerial images. All data was scaled to ensure that all variables could be plotted on the same axis. Tree cover bars above the horizontal line indicate periods in which tree cover increased from the previous extent, while those below the line indicate decreases in tree cover from the previous extent. Bar width is relative to the length of each period. Points above the horizontal line indicate values above the mean value, while those below the horizontal line are values below the mean value for the variable.

Mean annual summer (December to February) and winter (June to August) rainfall for each time period were plotted against *proportional* tree cover change between successive available aerial images (and where data overlapped on a timescale) (**Figure 9**



). Overall the sites appear to respond very differently to seasonal rainfall accumulation. There was a general decrease over time in mean summer rainfall at all but two sites (SabL and TseP). Mean winter rainfall fluctuated substantially over time across the park. There are evident seasonal rainfall differences; several high summer rainfall figures correspond with low winter rainfall values and vice versa.

Differences in high summer rainfall values are evident even on the same river: at SabL these coincide with decreases in tree cover, while at SabK they coincide with increases in tree cover. Tree cover in the three of the sites in the far north of the park (ShiV and both Shingwedzi River sites) and TimP decreases in the same period as relatively low winter-rainfall occurs. Overall, most sites seem to experience a decline in tree cover when mean summer rainfall is low, which may be expected in a summer-rainfall region. Low mean winter rainfall also almost always coincided with declines in tree cover. The greatest increases in tree cover usually coincide with above-average summer rainfall.

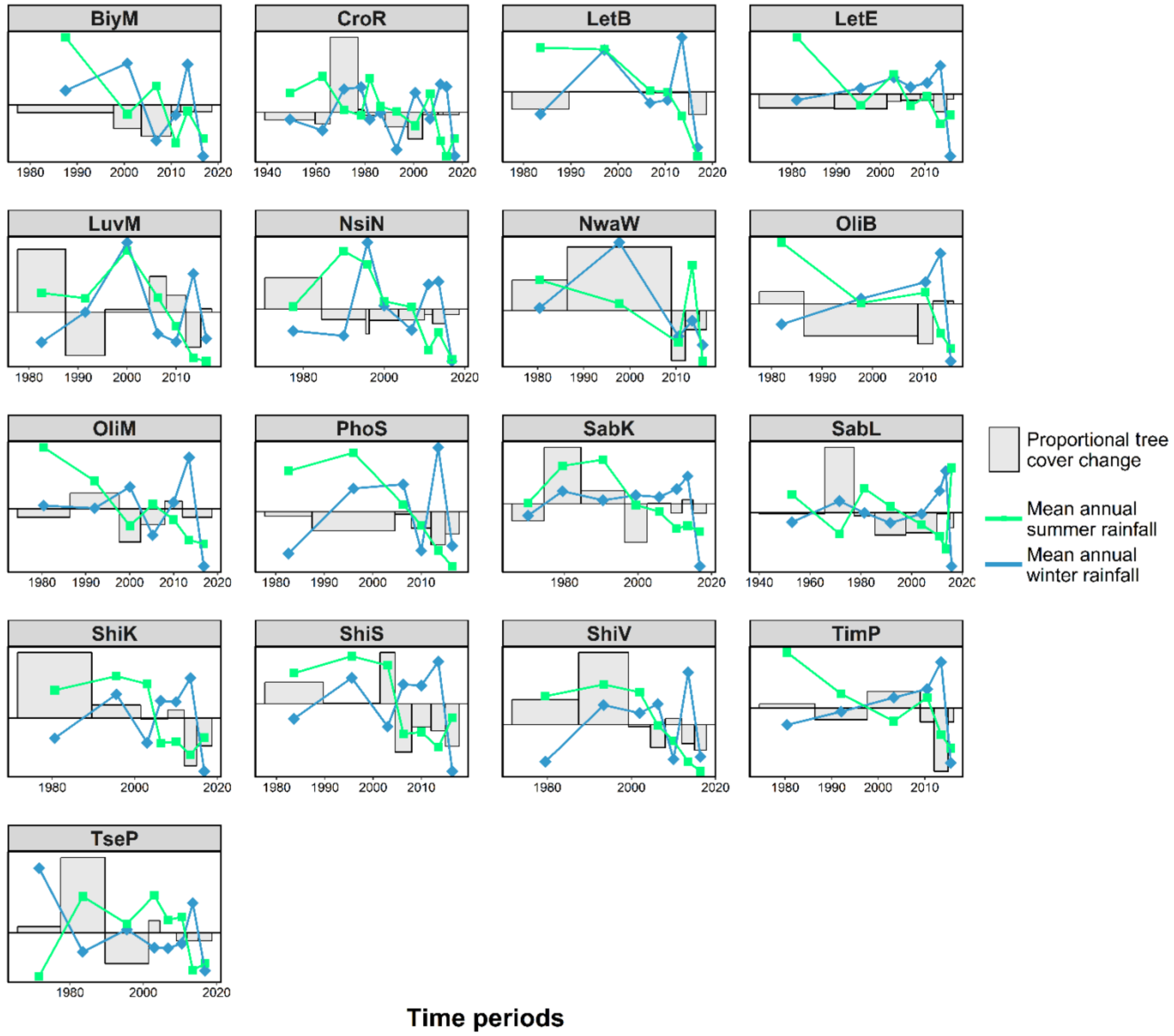


Figure 9. Mean annual summer and winter rainfall during each time period against tree cover change at the end of each time period between successive aerial images. All data was scaled to ensure that all variables could be plotted on the same axis. Tree cover bars above the horizontal line indicate periods in which tree cover increased from the previous extent, while those below the line indicate decreases in tree cover from the previous extent. Bar width is relative to the length of each period. Points above the horizontal line indicate values above the mean value, while those below the horizontal line are values below the mean value for the variable. Site CroT was omitted from the facet plot due to the zero values for tree cover

Multiple linear model

The initial multiple linear model run was veg_p_change ~ cltvflow + maxpeak + flowCV + flood + drought + cltvrain + rainCV + maxrain + meansumrain + meanwinrain. Following this the best-fit model with non-significant interaction terms removed based on the AIC stepwise model selection was given as veg_p_change ~ maxpeak + flowCV + cltvrain + maxrain (AIC = -316.86). This model was then run with site as a random effect and diagnostic plots revealed that there was sufficient homogeneity and normality of the residuals in the model. When geology and perenniality were added as mixed effects there was very little difference in the outputs compared to when site alone was used as a random effects model. The maximum flow (peak flood events) recorded and maximum monthly rainfall recorded were significant in explaining proportional tree cover loss *across all sites*, while CV of flow and cumulative rainfall were significant in explaining proportional tree cover increase across all sites (d.f. = 92) (**Table 5**). The adjusted R^2 value was 0.184, which is indicative of the high variability of the tree cover and environmental conditions across the sites. Site-specific trends, for which the multiple linear model cannot be applied, should be gleaned from **Figures 6–9**.

Table 5. Results of the most parsimonious multiple linear model run (d.f. = 92) assessing the effects of flow and rainfall on proportional tree cover change, with random effects (site, perenniality and geology) included in the model.

Response variable	Explanatory variable	Coefficient (mean change)	Std. Error	t-value	p-value
Tree cover change (proportional)	Maximum flow recorded (event)	≈ -0.0001	< 0.0001	-2.000	0.049
	CV Flow	0.0070	0.0033	2.157	0.034
	Cumulative Rainfall	≈ 0.0001	< 0.0001	1.996	0.049
	Maximum monthly rainfall recorded	-0.0005	0.0001	-2.560	0.012

Discussion

Eleven out of 18 sites experienced an overall decline in tree cover during the time period, while six sites showed a statistically significant downward trend. This finding adds credence to the anecdotal evidence that there has been an overall decline in riparian woodland extent and loss of large trees along KNP's rivers in the last few decades. The changes are not consistent in the rate of change but sites with higher proportional tree cover tended to experience greater losses in trees per annum. Changes were also not always gradual and fluctuations in tree cover dynamics were observed at several sites. The catchment areas of three of the sites with overall increases in tree cover (NwaW, BiyM and TseP) are fully contained in the park, while a fourth (TimP) has >90% of its catchment within protected areas. The lack of direct anthropogenic disturbances to these rivers could relate to a relatively undisturbed state. This may have contributed to the overall gain in tree cover, notwithstanding very recent declines. Anthropogenic disturbance in isolation is difficult to quantify but my results reveal that it may be an important factor which influences riparian habitat sensitivity.

Riparian woodlands in KNP have experienced dynamic changes and there are strong differences in the extent of riparian woodland, supporting the assertion that spatio-temporal vegetation change in KNP is complex (Rogers & O'Keeffe 2003). The pattern of increased tree cover between the mid-1960s and 1990s at several sites is inconsistent with an overall major decline in woody trees across the park in the same period noted by Scholes et al. (2003), but consistent with findings from a semi-controlled experiment outside of riparian areas, where CO_2 was determined to have played an important role in tree density increase (Buitenwerf et al. 2012). Following this, however, a decline was experienced between ca. 1990 and 2010 at most sites.

There is very little mean annual change in flow at most of the sites. Several authors have noted that flow in nearly all rivers flowing through KNP have been altered, predominantly showing declines, owing to changes in climate and thus rainfall patterns, increased abstraction upstream and land use changes (Breen et al. 2000; O'Keefe & Rogers 2003; McLoughlin et al. 2011; Pollard et al. 2011; Petersen et al. 2014). The results from this study show only a few sites experiencing an *overall* decreasing trend; the Crocodile being the only perennial river to do so. It is likely that recent large floods ca. 2000, 2012 and 2013 have influenced the linear trajectory of the flow trend for most sites. For example, the Letaba River sites both show an increasing trend and yet flow ceased in the Letaba River over four decades ago and it has since been regarded as non-perennial with the highest flow CV of KNP's main rivers (Carter & Rogers 1995; Heritage et al. 2001b; Freitag-Ronaldson & Foxcroft 2003; O'Keefe & Rogers 2003; Pollard et al. 2011). The increasing trend in river flow at the Sabie River sites is likely an artefact of recent floods. Even other metrics such as the number of low-flow days in KNP rivers do not show a consistent decrease over time. The sustained flow and consistency of flow cannot be accounted for well in long-term trends and this is likely to be more of a concern for park management in maintaining 'natural' flow regimes.

Overall, each site responded differently to aspects of flow and rainfall. There was substantial variation even between sites of close proximity and/or on the same river. This is likely due to the complexity of riparian vegetation dynamics, the relationship between vegetation and the flow *regime*, substrate and biotic interactions, which are important for shaping riparian structure and sustaining ecological functioning (Carter & Rogers 1995). Overall, flow CV was statistically significant in explaining increased riparian tree cover across the park. At a smaller scale, the sites which experienced an *overall* increase in vegetation in the study time period were mostly non-perennial, which have a high flow CV (Rossouw et al. 2005), or sites on the Letaba and Olifants Rivers, which have the highest flow CV of the park's large rivers (O'Keefe & Rogers 2003). This illustrates that consistent stream discharge (particularly in non-perennial rivers) is not vital in maintaining ecological functioning, as asserted by several authors. Instead, flooding appears to play a far more important role in reducing riparian tree cover. That said, the Olifants River sites show a negative trend in vegetation cover and increased CV in flow may have had a role to play in that. Peak (maximum) flow events (despite the flow record gaps) and peak (maximum) monthly rainfall were significant in explaining losses in trees across all sites. It is clear that LIDs, particularly the mega-flood of February 2000, left an imprint on the park's rivers, leading to a decline in tree cover at several sites, mostly in the southern region of the park. Had full flow records been available, no doubt peak flow events would have had an even greater impact if the trends are anything to go by. The flood of that year is said to have led to the greatest declines in riparian vegetation (Heritage et al. 2001; Ayres 2012) and the decreasing trend at many sites subsequent to ca. 2000 corresponds with this (**Figure 2**). Further large floods in 2012 and 2013 also caused substantial changes to rivers and riparian vegetation (in the Sabie River) (Milan et al. 2018). In this study, sites in the north of the park appear to have been particularly impacted by these recent floods, showing the spatial variation in flood effects across the park.

The effects of drought are difficult to elucidate. Only the two northernmost sites (LuvM and ShiV) and SabK experienced gains in tree cover with a high frequency of low-flow days per year. The worst drought during the study period, in 1991/2 was reported to have resulted in tree mortality only on the Sabie and Luvuvhu Rivers (Botha 2001; O'Keefe & Rogers 2003), which was also evident in this study for the LuvM site and possibly also the SabL site. It may be the fact that these rivers have the highest proportion of riverine woody vegetation in KNP and thus a greater probability of losing more trees (Carter & Rogers 1995). This corresponds with the results from this study where sites with greater tree cover showed greater declines in vegetation, likely because there are simply more trees vulnerable to damage, dieback or removal due to their greater abundance. It is possible that certain species were particularly affected. For example, sycamore figs are especially vulnerable to drought and suffered in the droughts of the 1990s (State of Rivers Report 2001; O'Connor 2010b; Marnewick et al. 2015). A greater number of low-flow days per annum was broadly associated with decreasing tree cover. Counterintuitively four sites with high tree cover (LuvM, SabK, ShiV and ShiK) experienced increases in tree cover with a high number of extreme low-flow days. The following periods all showed declines in tree cover, indicating a possible time lag in the effect of droughts, which manifest over a prolonged period, possibly exacerbated by other disturbances (Viljoen 1995; O'Connor 2001, 2010b; Kotzé 2015). In contrast to drought, floods are strongly episodic causing rapid changes and especially through the physical removal of trees (Naiman & Decamps 1997).

Flow regimes of KNP rivers are additionally determined by long-term climate. Results from this study show that tree cover overall appears to be stimulated by high cumulative rainfall, while generally periods of high rainfall CV coincided with losses in vegetation. This indicates that riparian areas benefit from more consistent rainfall, but rainfall in KNP is already highly seasonal (Zambatis 2003) and becoming increasingly so, with extended dry periods (van Wilgen et al. 2016), decreases in summer rainfall and lower annual rainfall at most sites. Furthermore, low winter rainfall almost always coincided with losses in tree cover across the park. These, combined with the negative overall effect of peak flow events, which are likely to increase (van Wilgen et al. 2016; Fitchett 2018), means trees may struggle to access necessary water in drier months if baseflows are not maintained from summer rainfall, presenting possible challenges for riparian tree persistence in the future.

The stress associated with lower winter base flows and more regular floods are likely to change riverine characteristics and result in consequences for other biota (Milan et al. 2018) to a greater extent than in upland savanna habitats (Gillson & Ekblom 2009). While riverine conservation has become central to the core conservation functions of KNP and has formed the basis of research programmes prior to 2000 (Breen et al. 2000; McLoughlin et al. 2011; Pollard et al. 2011), non-perennial rivers have received little attention. Habitats adjacent to non-perennial rivers may be worth focussing on to meet biodiversity conservation goals considering the generally reduced impact of LIDs on riparian woodlands along the non-perennial rivers in this study. The quandary that arises is that riparian and river research requires long-term study (O'Connor 2010b), yet changes to these systems may occur within time-frames too narrow to reflect in research. Long-term monitoring will be the only reliable method to detect, assess, and validate predicted changes in riparian ecosystems and thus provide a useful basis for adaptive management of riparian systems (Nilsson & Berggren 2000).

While this study explored the interactions between riparian trees and flow and rainfall, elephants and fire may also to be important in riparian systems. Elephant numbers in KNP have increased exponentially in the last century, resulting in disproportionate effects on woody vegetation structure across habitats (Eckhardt et al. 2000; Scholes et al. 2003; O'Connor 2010b; Asner & Levick 2012; Ferreira et al. 2012). Elsewhere in sub-Saharan Africa, they have affected riparian habitats, severely in some instances, even prompting interventions to protect vulnerable habitats (O'Connor et al. 2007; Moe et al. 2009; Smit & Ferreira 2010; O'Connor 2010b). Fire, while rare in riparian areas, ought to be considered due to its ecological implications which can be far-reaching in riparian areas (and as a result of their spatial configuration), which are able to influence fire patterns across large spatial scales (Pettit & Naiman 2007b; Smit & Archibald 2019). Fire appears to be more impactful in riparian habitats following floods when wood debris provides adequate fuel (Pettit & Naiman 2007a, 2007b). Neither fire nor elephant damage in isolation is likely to affect large (>5 m) riparian trees (Midgley et al. 2010), but rather in an additive effect (Vanak et al. 2012), however, both are likely to impact seedlings and younger trees, as evident from exclosure experiments and visual observations (Asner & Levick 2012; Wigley et al. 2014). Ironically, the higher elephant densities and overall herbivory around rivers may act to reduce the effects of fire in riparian areas through loss of fuel load (Smit & Archibald 2019), thus reducing the combined effect. While some sites were undoubtedly largely affected by the flood of 2000, this cannot explain changes further from the time of the flood. Declines are particularly noticeable after 2000 but cannot all be linked to flow. Large floods are likely to scour areas making them less susceptible to subsequent floods (D Thompson *pers. comm.*). It is likely then, that other factors, particularly herbivory (driven mostly by elephants) and fire have played a role in the declines in riparian vegetation post-flooding in conjunction with recent droughts and closure of artificial water points (see Gaylard et al. 2003; O'Connor et al. 2007; Smit & Archibald 2019) which may have driven up elephant density around rivers (Smit & Ferreira 2010). It should be noted that there are several other spatio-temporally nested drivers of vegetation dynamics of importance which should be considered in the wider view of these habitats (e.g. wind, age, creepers, lightning, insect herbivory; O'Connor 2010a, 2010b).

Study limitations

Gauging stations are exposed to severe natural phenomena and flooding, primarily, has damaged some of the stations to the point where gauge functionality has ceased, resulting in periods, often of several months, for which data were not recorded (Smithers et al. 2001). Furthermore, some stations have since been decommissioned or were never repaired following flood damage (J Venter *pers. comm.*). Because of the floods, flood peak values and thus mean values were estimated as far above the actual and modelled data (Heritage et al. 2001). The resultant damage from the floods (in addition to other reasons for data losses) leads to gaps in data at possibly the most crucial time for analysis of flooding and general flow impacts. Any gaps resulted in lower deseasonalised flow figures in some cases, possibly reducing the effects of flood events. Unfortunately, only sophisticated modelling could potentially mitigate some of these gaps. Furthermore, six of the sites have relatively major tributaries (only two perennial) which flow into the study sites below the weirs which would have implications for riparian vegetation dynamics in flood events or periods of high flow. Without sophisticated catchment modelling these are challenging to account for and the flow measures would therefore be underestimates during high flow periods. In the case of this study, it is hoped that available and reliable data were sufficient to draw on for analyses. Fire scar data (Didan 2015), as a measure of fire frequency, for the riparian polygons for the period

2000–2014 were sourced from SANParks. However, given the granularity of the data (250 m), there was no way of concluding if fires had indeed penetrated the riparian zone itself. These data were thus excluded from the analyses and older data were not requested. Similarly, elephant data for KNP is closely guarded and a request was not made for the data given the possibly long time frame associated with accessing the data after requesting them, and the short time frame for the project analyses.

Historical aerial imagery is not available consistently across space and time for the study area. It also varied in scale and quality/resolution, with high-quality imagery too time-consuming to access. The method to measure tree cover was employed due to the nature of the historical imagery and the fact that modern object-based extraction tools would not be able to fulfil the aims of the methodology on monochromatic images. Random point sampling is unbiased but requires high density sampling. For example, at the CroT site, no tree cover was recorded although there were some trees in the image. Additionally, loss of many large trees along the Olifants River in the last decade has been documented (Botha 2013, 2014; Marnewick et al. 2015) and yet the results here indicate only minimal loss at OliB and an increase at OliM. The results of random sampling may therefore give an assessment of the site-level changes, but may fail to accurately capture change at the scale of the river.

Finally, the lag time/s between rainfall and LIDs and vegetation responses are difficult to account for, especially without high temporal resolution of aerial imagery. By binning data into time periods and using tree cover at the *end* of each period, it is hoped that the lag effects are accounted for to some extent. I acknowledge that there may certainly be methods for accounting for lags with greater accuracy, one of which may have been to use a higher density of sampling points.

Conclusion and conservation implications

Tree cover extent in KNP's riparian zones has fluctuated in the past 80-odd years and is no different to other savanna systems in their dynamic nature. The variable trends of these changes, not only temporally, but also spatially, further relates to the spatial heterogeneity and diversity of KNP. Observations that riparian woodlands are decreasing are not unfounded and this study reveals that the pattern of decline has occurred across all regions of the park and on rivers with different flow regimes and anthropogenic stressors. Where woodland extent has increased, there appears to be a link to lack of anthropogenic disturbance indicating systems free of human alteration with smaller catchment areas are less prone to riparian vegetation loss due to factors driven by the flow regime.

It is difficult to ascertain the exact drivers of ecosystem change from a once-off historical analysis, however, this study has attempted at least to reveal some of the likely drivers and identify associated trends thereof. While each site responded differently to aspects of river flow and rainfall, riparian woodlands as a whole showed particularly significant responses to large flood and high monthly rainfall, which overall, seem to have driven declines in tree cover, and variability of flow and cumulative rainfall which seemed to be important predictors in driving tree cover expansion. These are natural phenomena management has little control over, and in all likelihood, the extremes and variability experienced in rainfall and river flow are likely to increase in line with climate change predictions for the region. Ideally a full ecosystem modelling framework ought to be utilised to factor in nested drivers of riparian woodland dynamics. Of interest would be ascertaining what impact internal stressors, such as elephants and fire and their management, have had on riparian ecosystems and whether management could be adapted initially. A study of this nature should also be repeated in several decades. With the rapid advances in remote sensing technologies, a high-resolution, detailed study may reveal a clearer picture of riparian dynamics and their sensitivity to natural phenomena.

The loss of riparian trees should not be viewed in isolation. In some areas, this loss may be equal to that of many upland areas. The concern, however, is due to the tiny fractional area riparian habitats occupy. As much as park management seeks to enforce heterogeneity and encourage flux, the changes detected may be of conservation concern and require active intervention. Conservation of riparian vegetation is critical to river system integrity (Naiman & Decamps 1997; Naiman et al. 2005), and thus has implications on a wide spatial scale and for many taxa. It is unclear as to what level of concern the changes in riparian systems are. Furthermore, it is imperative to understand the critical economic role KNP plays in the national park network, being one of a few parks that turn a profit and thus fund conservation action at smaller parks (Biggs et al. 2014). Turpie & Joubert (2001) found that riverine state played a pivotal role in visitation by tourists and that many would reduce the time spent (and thus reduce expenditure) if rivers (and supposedly riparian areas as one indicator) were degraded to a certain point. Considering the economic value of KNP not only to the South African National Parks (SANParks) but to the country, it appears that prioritisation of these systems is critical.

Ideally, the park seeks to promote adaptive management that enhances heterogeneity and thus flux in systems (Pickett et al. 2003; Rogers & O'Keeffe 2003; McLoughlin et al. 2011; Pollard et al. 2011). The persistence of large trees is vital in savanna ecosystems (Vanak et al. 2012), and there may come a point when a severe loss in large trees occurs and intervention is required to ameliorate that to ensure a desired state, and this is likely to require active and possibly innovative management. The park will have to continue looking to its neighbours and re-ignite negotiations with water boards, industry and landowners to ensure catchment-wide strategies which promote and ensure instream flow requirements in accordance with the Water Act and for biodiversity maintenance (Freitag-Ronaldson & Foxcroft 2003; Hughes & Hannart 2003; O'Keefe & Rogers 2003; Seavy et al. 2009; Pollard et al. 2011). It may not be viable and considering the climate change predictions and continued pressure on water and riparian resources, the only option to park management could be to monitor riparian areas, collect data and do the best they possibly can to effectively manage the systems within their capabilities and mandate.

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