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Rainfall, peak river flow and flow variability drive spatio-temporal change in the extent of riparian woodland in an African protected area savanna

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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, South Africa) over the last century. A multi-decadal analysis was conducted to identify trends in extent and possible drivers of riparian woodland change. Aerial and satellite imagery (1936–2018) were used to quantify changes in the extent of riparian woodland at 18 sites on 14 rivers in KNP. These changes were compared in a multivariate time-series with river flow and local rainfall. Particular attention was paid to cumulative flow effects, as well as the frequency and magnitude of large infrequent disturbances such as droughts and floods. Riparian tree cover fluctuated over the time period, and the trajectory of change varied between sites. Most (11) sites experienced a decrease in overall riparian tree cover over ~80 years, with these declines being significant at six sites. Peak flow and maximum rainfall events were strongly associated with these decreases, indicating that flood events are potentially the biggest driver of tree loss from the system. Indeed, the mega-flood event of 2000 and subsequent large floods have resulted in substantial declines in riparian woodland extent in recent decades. Alternatively, flow variability and cumulative rainfall significantly influenced woodland expansion in isolated cases. With global change models predicting more erratic rainfall and an increased likelihood of large infrequent disturbances, together with increasing demands to abstract more water, the long-term future of these dynamic habitats and their associated biota here is uncertain.

KEYWORDS
Kruger National Park, large infrequent disturbances, natural hazards, riverine conservation, vegetation dynamics

1 | INTRODUCTION

In sub-Saharan savannas, riparian woodlands are characterised by relatively dense vegetation comprising primarily large, evergreen trees in sharp contrast to the surrounding upland vegetation (Monadjem & Reside, 2008), making them structurally and floristically intermediate between tropical forest and savanna (Hughes, 1988) and thus important ecotones in the landscape. 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).

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, 2010). Due to their unique nature within landscapes and the importance of riparian systems, 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 due to human impacts. Riparian zones are typically highly variable and unpredictable ecosystems (Naiman et al., 2005; O'Keefe & Rogers, 2003). Flooding and periods of low flow are critical for many riparian species and maintain ecological integrity (Milan et al., 2018; Poff et al., 1997).

The timing, duration, frequency, magnitude and intensity of flooding are the primary aspects of river flow that shape riparian vegetation structure and associated biota, through interactions with fluctuating water levels, channel structure and substrate characteristics (Hughes, 1988; Naiman et al., 2005; O'Connor, 2001, 2010; Poff et al., 1997; Rogers & O'Keeffe, 2003). Flooding can remove plants through abrasion or erosion and/or undercutting of substrata or by shear force. Consequently, the topography and geomorphic template supporting riparian woodlands are constantly changed by river flow, creating a unique and shifting spatio-temporal mosaic (Gregory et al., 1991; Milan et al., 2018; Milan et al., 2020; Naiman & Decamps, 1997).

The return interval, duration and intensity of such disturbances are 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 also induce stress and dieback in many riparian plant species (O'Connor, 2001, 2010), despite their inherent adaptions to fluctuating water availability. Variable river discharge leads to a highly distinct and dynamic structure within the landscape, supporting only species that are able to cope with these significant disturbances (Gregory et al., 1991; Naiman et al., 2005). Long-lived 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 tree 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 (Breen et al., 2000; Naiman et al., 2005; Naiman & Decamps, 1997; Rogers & O'Keeffe, 2003).

There is concern over the persistence of riparian woodland in South Africa's largest terrestrial protected area, the Kruger National Park (KNP), with repeat fixed-point photos and limited aerial imagery showing a decline in the extent of riparian woodland since ca. 1980s (Figure 1). Concurrently, the rivers flowing through KNP have been increasingly modified due to growing anthropogenic pressures outside the park boundaries (O'Keefe & Rogers, 2003; Pollard, du Toit, & Biggs, 2011). Changes in climate, particularly in the frequency, intensity and magnitude of extreme weather events (including and as a result of tropical cyclones and dry period such as those during strong El Niño patterns) and seasonal variability, are also likely to intensify (van Wilgen et al., 2016), with potential consequences for riparian ecosystems.

Six large perennial rivers (viz Luvuvhu, Shingwedzi, Letaba, Olifants, Sabie and Crocodile) and many smaller, non-perennial rivers and streams make up the ~31,500 km of rivers within the boundaries of KNP (O'Keefe & Rogers, 2003). These drain seven sub-catchments and three primary river catchments. The flow regimes of most rivers regionally are highly unpredictable over time with a large coefficient of variation (CV) resulting in vegetation communities that are dynamic and varied (Rogers & O'Keeffe, 2003). In KNP, river characteristics, catchment areas and flow regimes, varied geology and climate gradients across the park contribute to highly variable riparian vegetation structure (Gaylard et al., 2003; Milan et al., 2018; O'Keefe & Rogers, 2003). KNP is orientated in such a way that the majority of the length of the rivers flowing through the park that emanate outside of its boundaries are susceptible to a variety of anthropogenic alterations (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 been severely modified, such that only one main river—the Sabie—is considered *truly* perennial (Pollard et al., 2011). This modification is thought to exacerbate flow variability as a result of extreme climatic events, leading to a deterioration in quality and quantity of biota and, certainly in the last two decades, altering riparian communities on some rivers (Marnewick et al., 2015; O'Keefe & Rogers, 2003; Pollard et al., 2011; Rogers & O'Keeffe, 2003).

By virtue of its size, KNP conserves a sizeable proportion 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. While the effects of the exceptional flood event of 2000 in the region have been widely documented (see Ayres, 2012; Heritage et al., 2001; O'Keefe & Rogers, 2003; Parsons et al., 2005; Rountree et al., 2000; Smithers et al., 2001), these have focussed on geomorphological impacts and general habitat change and are spatially and temporally restricted with limited historical evaluation. Little work, even elsewhere, has assessed the *historical trends* in riparian woodland extent, which is useful for determining future management decisions (Vanak et al., 2012). Quantifying changes at larger spatial and temporal scales, and assessing the potential drivers thereof, may reveal the sensitivity of these riparian woodlands to changing environmental conditions driven by climate and/or anthropogenic disturbance.

Here, we used KNP as a case study to assess changes and associated drivers of riparian woodland cover. Specifically, we sought to elucidate changes in riparian woodland tree canopy cover (hereafter, 'tree cover' and 'woodland cover' used interchangeably) over time and link this to river flow and rainfall. Based on anecdotal evidence, we hypothesised an overall decline in riparian woodland extent primarily due to large infrequent disturbances such as drought and

FIGURE 1 Repeat satellite imagery showing changes in riparian woodland extent over time i. Top: Luvuvhu River in May 2006 (left) and June 2007 (right); centre and bottom: Olifants River in March 2009 and July 2013. *Imagery source*: Google Earth/DigitalGlobe (2018).

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; O'Keefe & Rogers, 2003; Pollard et al., 2011), large infrequent disturbances have likely been exacerbated by anthropogenic pressures, although these were not quantified in this study. Given the highly variable nature of the riverine areas within KNP (Carter & Rogers, 1995), it was predicted that both change in woodland cover and the environmental variables responsible thereof would vary strongly at the local scale. Vegetation cover changes were assessed in relation to concurrent flow and rainfall records to assess potential relationships.

2 | METHODS

2.1 | Study area and site selection

The KNP is located in north-eastern South Africa (Figure 2), 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; Mabunda et al., 2003). The park experiences predominantly summer rainfall in the form of discrete, brief thunderstorms 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 (SANParks, 2018; Venter et al., 2003; Zambatis, 2003, 2006).

Eighteen sites were selected for assessment based on the locations of South African National Department of Water and Sanitation (DWS) hydrological flow gauging stations (Figures 2 and S1). For the sake of brevity, site names were derived from the first three letters of the river name followed by the first letter of the DWS gauging station name: Luvuvhu–Mutale (LuvM); Shisa–Vlakteplaas (ShiV); Sirheni–Mphongolo (SirM); Shingwedzi–Kanniedood (ShiK); Shingwedzi–Silwervis (ShiS); Tsendze–Pioneer Dam (TseP); Letaba–Engelhardt Dam (LetE); Letaba–Black Heron (LetB); Olifants–Balule (OliB); Olifants–Mamba (OliM); Timbavati–Piet Grobler Dam (TimP); Nwanedzi–Wenela Drift (NwaW); Sabie–Kruger Gate (SabK); Sabie–

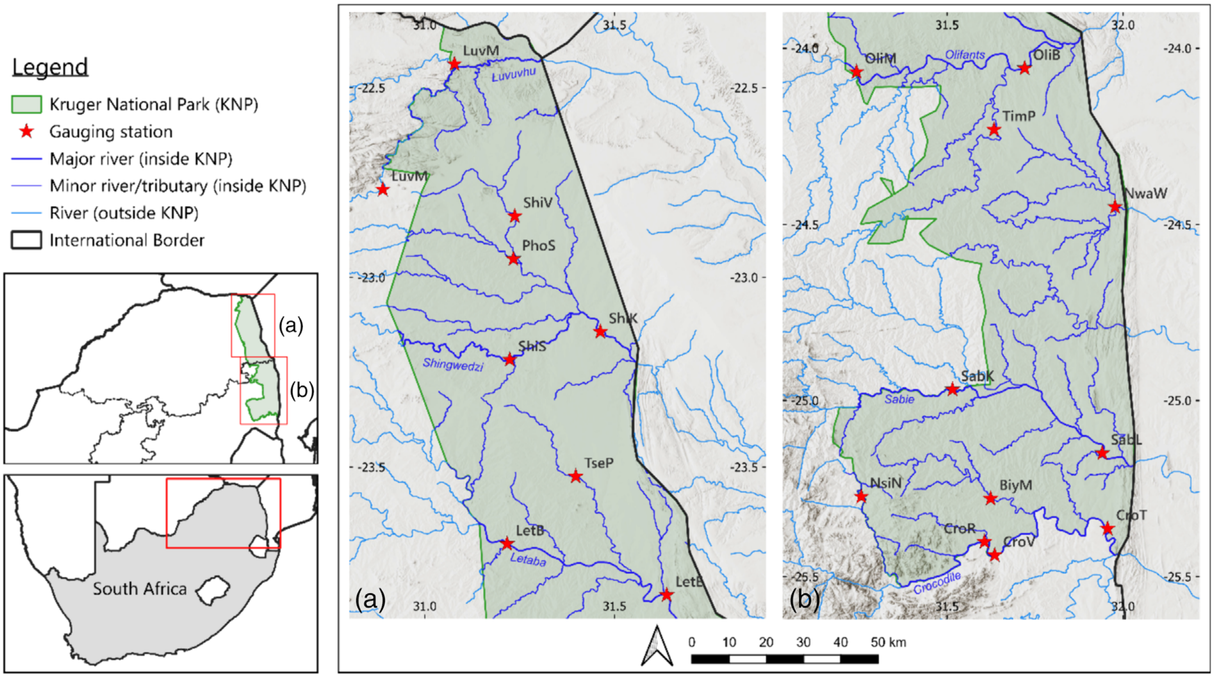

FIGURE 2 Locations of 18 selected study sites within the Far North, North (a), Central and Southern sections (b) of the Kruger National Park. The names of major rivers are indicated.

Lower Sabie Rest Camp (SabL); Nsikazi–Kruger National Park (NsiK); Biyamiti–Mbyamithi (BiyM); Crocodile–Tenbosch (CroT); Crocodil–Riverside (CroR); and Crocodile–Thankerton van Graan se Dam (CroT). These span five large perennial rivers and nine non-perennial rivers, in seven sub-catchments intersecting KNP. Owing to their inherent variable nature, sites were not treated as replicates (Figures 2 and S1).

2.2 | Riparian woodland cover determination

Gauging station spatial location data were obtained from the DWS data repository. The station vector points were snapped to the nearest river line obtained from the National Geospatial Information (NGI) 2016 topographical vector dataset. 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. Within the 5-km radius, 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 as per the South African Protected Areas Database (DEA, 2018) to create 18 approx. 10-km-long river reach polygons. Section ranger homesteads and tourist facilities such as rest camps and picnic sites were excluded from the polygons to avoid bias caused by trees that may have been planted or been buffered from flooding or with a greater drought tolerance due to possibly being watered artificially.

Within each polygon, riparian area boundaries were delineated by manually digitising riparian areas from Google Earth 2016–2018 Landsat 8 imagery through visual identification of typical dense riparian woodland features and visible soil differences from surrounding savanna (which has a sharp colour and texture contrast), including parts of the river macro-channel to account for possible historical changes in the channel structure, and some leeway in the terrestrial component to account for historical change. These new polygons totalling 5 021 ha were used for analyses.

Riparian woodland extents at selected sites at different times (1936–2018) 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) (S2) for the years 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 $(0.1 \times \mathit{area\ of\ polygon}\,(\mathit{ha}))$ of random points separated by at least 100 m were generated using a point count sampling strategy $(n = 502)$. A 5-m buffer was applied to each point to create a $78.5\ \mathrm{m}^2$ circular plot. Each plot was inspected for the presence of any part of an individual distinguishable large tree (through identification of a dense, continuous identifiable canopy area) and repeated for every available aerial/satellite image of sufficient quality. A binary score was used for the absence or presence of an individual tree, based on the visible canopy. Large trees could easily be distinguished from newer imagery due to the sharp contrast afforded by the high resolution, however, they could not always be fully differentiated from bush clumps in older photographs, other than sometimes appearing darker. The contrast was digitally adjusted to assist differentiation. The proportion of riparian woodland 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. All geospatial functions were conducted in QGIS (QGIS Development Team, 2018).

2.3 | 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 (DWS, 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 (S1). Only sites with data reliability (an accuracy metric determined by DWS) 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 (S3).

2.4 | Data and statistical analyses

Data and statistical analyses were conducted in R (R Core Team, 2017) using the *tidyverse* (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 were smoothed using locally-weighted scatterplot smoothing (LOESS) regression. Due to locally variable characteristics of the sites throughout the park, the specific trends for each were derived individually.

Overall change (difference in woodland cover) was obtained by calculating the slope between the first and last woodland cover value at each site for the entire period. Mean annual change in woodland cover at each site was compared to the site's median woodland 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 woodland cover (Table 1). These variables were used for one-way analysis of variance (ANOVA), followed by post hoc Tukey HSD tests where necessary, to assess if there were significant differences in woodland cover and woodland 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 failed a Welch one-way ANOVA or Kruskal–Wallis test was used.

Due to the potential impact of several, interacting variables that we hypothesised would interact to result in woodland change, multiple linear regression was used to determine if any of the variables explained changes in woodland 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).

3 | RESULTS

3.1 | Woodland cover change

All 18 sites experienced fluxes in riparian woodland cover over the course of the period analysed (Figures 3 and 4). Median woodland 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 woodland cover change per annum within each time period between sites as determined by one-way ANOVA tests. In terms of overall change in tree cover in the period analysed (range = −0.59%–0.23% Δ), tree cover increased at six sites and decreased at 11 sites, with one site (CroT) showing no change (Figures 3 and 4). Of those sites that experienced an increase, only one (OliM) was on a perennial river.

In terms of the trend in woodland cover, rather than net change, three sites (NwaW, TimP and TseP) increased (only TseP was significant), while there is a decreasing trend at 14 sites, six of significant (LuvM, NsiN, OliB, PhoS, SabK, SabL and ShiS). Another pattern is that of decreasing woodland cover from the 1990s onwards at most (16) of the sites (Figure 4). The highest tree cover during the study period, being 79%, was recorded at SabK in 1996. Other sites with high tree cover (defined as >40%) at some point in time were LuvM, the Shingwedzi River sites, ShiV, NwaW and NsiN. There was low tree cover (defined as <15%) at both Crocodile River sites, both Letaba River sites, both Olifants River sites, SabL and TimP. Several sites (BiyM, CroR, NsiN, PhoS, SabK, SabL and ShiK) showed a pattern of increasing woodland cover towards the middle of the study period (1960s–1990s); that is, the highest woodland cover was recorded at an intermediate (rather than terminal) period within the analysis at 10 sites (Figures 4 and 7).

TABLE 1 Variables created from raw river flow and rainfall data and used in ANOVAs and multiple linear regression model.

Data category	Variable	Description
Site characteristics	site	Code for site name (see S1)
	region	KNP region[a]
	perenn	Perennial/non-perennial[b]
	order	Strahler's Stream Order (Strahler, 1957)
	geology	Primary underlying simplified geology—basalt or granite.
	veg_p_change	Proportional change in woodland cover from last recorded woodland 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, as defined by the authors) per year during the time period between each successive aerial image per site.
	drought	Number of low flow events (< 0.1× mean flow, as defined by the authors) 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.

[a] Olifants River forms the border of the central and north regions in KNP. Olifants River sites were classified as central in this study.

[b] Based on the most current literature, not historical flow characteristics.

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 5). Sites with higher median tree cover across the entire study period generally tended to lose more tree cover per year. SabK and ShiS show 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.

3.2 | Hydrological changes

Six of the sites (BiyM, both Crocodile River sites, 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 6). The remainder of the sites all show an increasing trend in mean monthly flow pear year (mean of 12 months per year), of which six were statistically significant (both Letaba River sites, NsiN, both Sabie River sites and ShiV). Flood events increasing in severity are not supported from data from the flow records; however, the graphs in Figure 6 indicate more regularly occurring high-flow events at four of the sites (NsiN, OliM, SabK and ShiV).

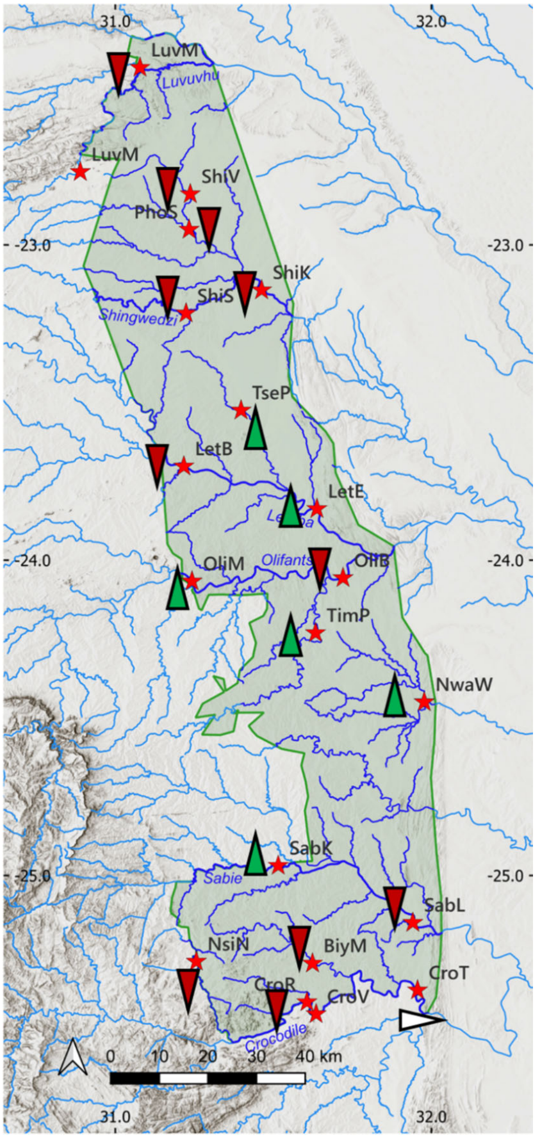

FIGURE 3 Spatial representation of overall riparian tree cover change at each study site between the first and last available imagery per site. Red arrows indicate a decrease in net riparian tree cover and vice versa for green arrows pointing up. CroT had a net zero change, indicated by the white arrow pointing to the right.

3.3 | Spatio-temporal trends in flow, rainfall and tree cover

The trends of tree cover, deseasonalised river flow and rainfall were spatio-temporally variable (Figure 7). No consistent relationships are apparent at several sites. For example, the rainfall and resultant flood event of 2000 seemed to have had little effect on tree cover at both Letaba sites; however, a decrease in rainfall between 2005 and 2010 preceded a decline in tree cover. At LuvM, high flow ca. 2000 appears to have spurred an increase in tree cover, but this was not the case ca. 2014 when subsequent high flow events occurred (prior to a significant El Ninõ period from 2015 to 2016). 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 3), after a period of lower rainfall and decreased flow. Tree cover appears to decrease ca. 2000 at five sites (TseP, SabK, both Shingwedzi River sites, and ShiV). Four sites (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. 2010–2012, although some sites experienced earlier declines (i.e., SabL, NsiN and LuvM) (Figures 4 and 7).

3.4 | 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 2). 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, are in the Supporting Information.

4 | DISCUSSION

Eleven out of 18 sites experienced an overall decline in tree cover that was not statistically significant, while six sites showed a statistically significant downward trend during the time period, ranging from 23 to 57 years depending on the site. This finding adds credence to the anecdotal observations that there has been an overall decline in riparian woodland extent and loss of large trees in the riparian zones of 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 90% of a fourth (TimP) catchment is within the protected areas. The lack of direct anthropogenic disturbances to these rivers could relate to a relatively undisturbed state. Further, the catchment areas are also substantially smaller than most

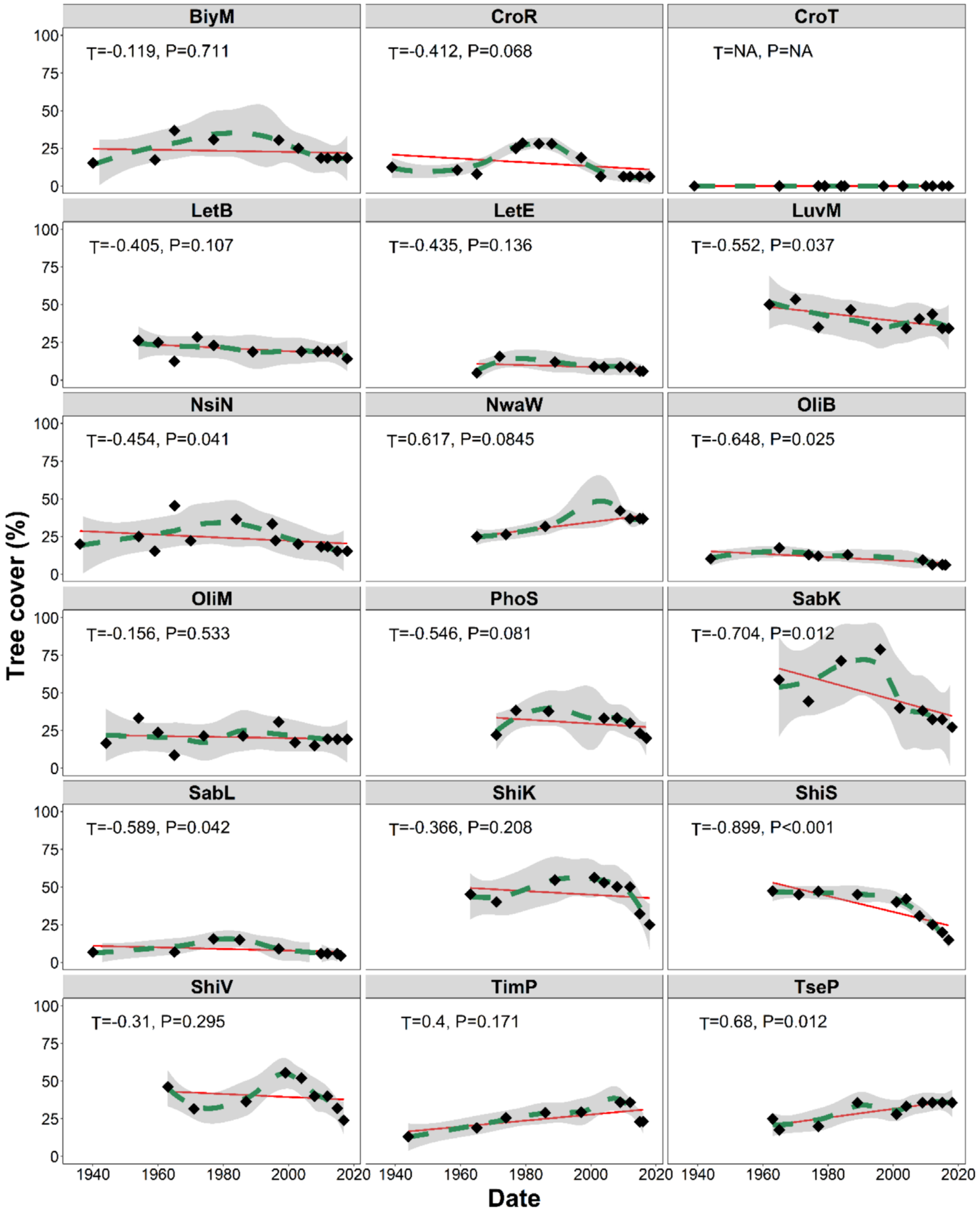

FIGURE 4 Tree cover change trends at each of the study sites. Points represent the measured tree cover percentage at a given time. A LOESS curve with a 95% confidence band was fitted (green line with grey band) to detect the smoothed trend over time, while linear regression line was fitted (red line) to the data simply to visually display the overall trend at each site. The Mann–Kendall tau coefficients (τ) for monotypic trends ($+ =$ upward, $- =$ downward) and *P* values at the 95% confidence interval are given.

of the other rivers' catchment areas. Combined, these may have contributed to the overall gain in tree cover, notwithstanding recent declines, as well as being at less risk to riparian damage due to lower flood intensity of smaller catchments. Anthropogenic disturbance in isolation is difficult to quantify, but our results reveal that it may be an important factor that 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,

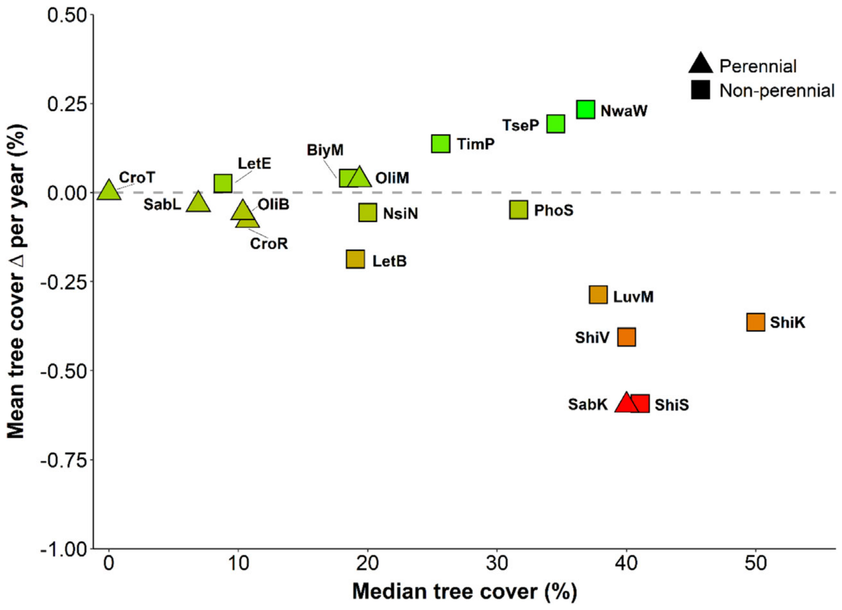

FIGURE 5 Change in tree cover per year versus the median tree cover percentage during the study period, for each site. Colours are graded red (loss) to green (gains) by mean tree cover change per year.

however, a decline was experienced between ca. 1990 and 2010 at most sites.

Statistically, there is very little mean change in annual flow at most of the sites. Several authors have noted that flow in nearly all rivers flowing through KNP has 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; Kassambara, 2018; McLoughlin et al., 2011; O'Keefe & Rogers, 2003; Pollard et al., 2011). 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 in mean flow and yet perennial flow ceased in this 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; Freitag-Ronaldson & Foxcroft, 2003; Heritage et al., 2001; 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 although long-term variation is not well captured owing to the lower data available. Even other metrics such as the number of low-flow (0.1 × DAF for a recorded period) 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. This consistency of flow is likely to be more of a concern for park management in maintaining ‘natural’ flow regimes in perennial rivers primarily due to its importance for biodiversity that relies on the aquatic habitats, as well as for ensuring hydrological balance both above the surface and in groundwater aquifers.

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, riparian substrate, river and channel morphology and biotic interactions, which are all important for determining riparian structure and sustaining ecological functioning (Carter & Rogers, 1995). Overall, flow CV was strongly correlated with increased riparian tree cover across the park. At a smaller scale, the sites that 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 the lack of consistent stream discharge (such as the case of non-perennial rivers) does not prevent the persistence of riparian woodland, at least in semi-arid savannas. Instead, flooding appears to play a far more important role in determining riparian tree cover, with the exception of a few sites. 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 large infrequent disturbances, 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. Complete flow records, unavailable in many cases due to structural damage to gauging stations, would have been valuable in confirming this around that time. The flood of that year is said to have led to the greatest declines in riparian vegetation (Ayres, 2012; Heritage et al., 2001), and the decreasing trend at many sites subsequent to ca. 2000 corresponds with this (Figures 4,7). Further large floods in 2012 and 2013 also caused substantial changes to rivers and riparian vegetation (Heritage et al., 2015; 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 that is latitudinally extensive. This could point to several factors that were not explored in this study, such as the role of channel morphology and basin characteristics. Channel morphology and associated stream energy, sediment

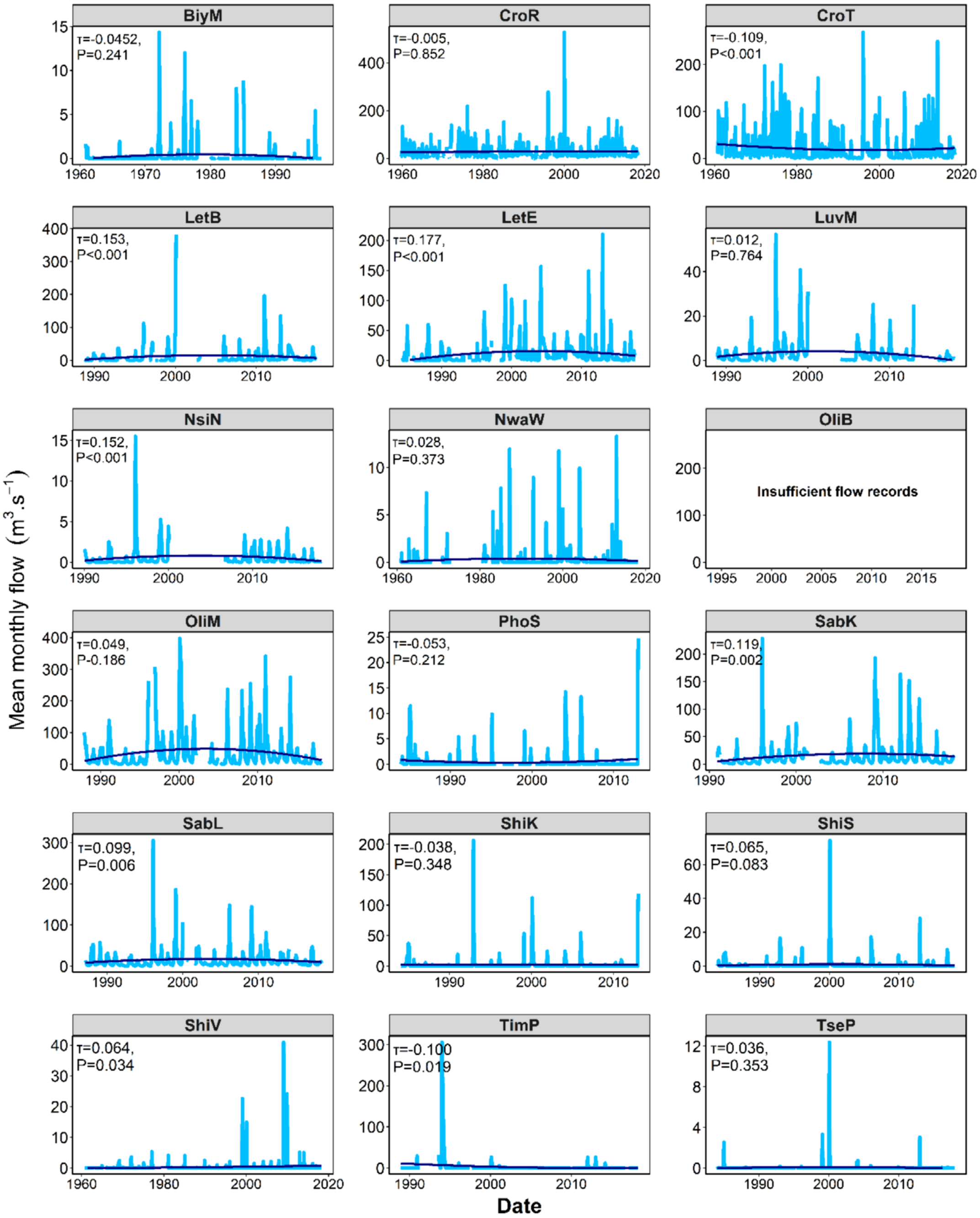

FIGURE 6 Mean monthly flow per year for each study site. A LOESS regression line (dark blue) was fitted to visibly depict the overall trend in flow, considering the continuous nature of the data. The Mann–Kendall tau coefficients (τ) for monotypic trend (+ = upward, − = downward) and *P* values at the 95% confidence interval are given. Site OliB did not have sufficient flow records for meaningful analysis.

depth and presence of bedrock will interact with stream flow to control vegetation composition and cover, especially in the river channel. This has been shown in detailed studies at small scales focussing on individual rivers (e.g., Heritage et al., 2015; Milan et al., 2018) and not at a landscape, or in the case of a large protected area like the KNP, park-level.

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 1991/1992, 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 simply have a greater probability of losing more trees (Carter & Rogers, 1995) as well the riparian macro-channel form of these rivers (allowing for a greater cross-sectional representation of trees). This corresponds with the results from this study where

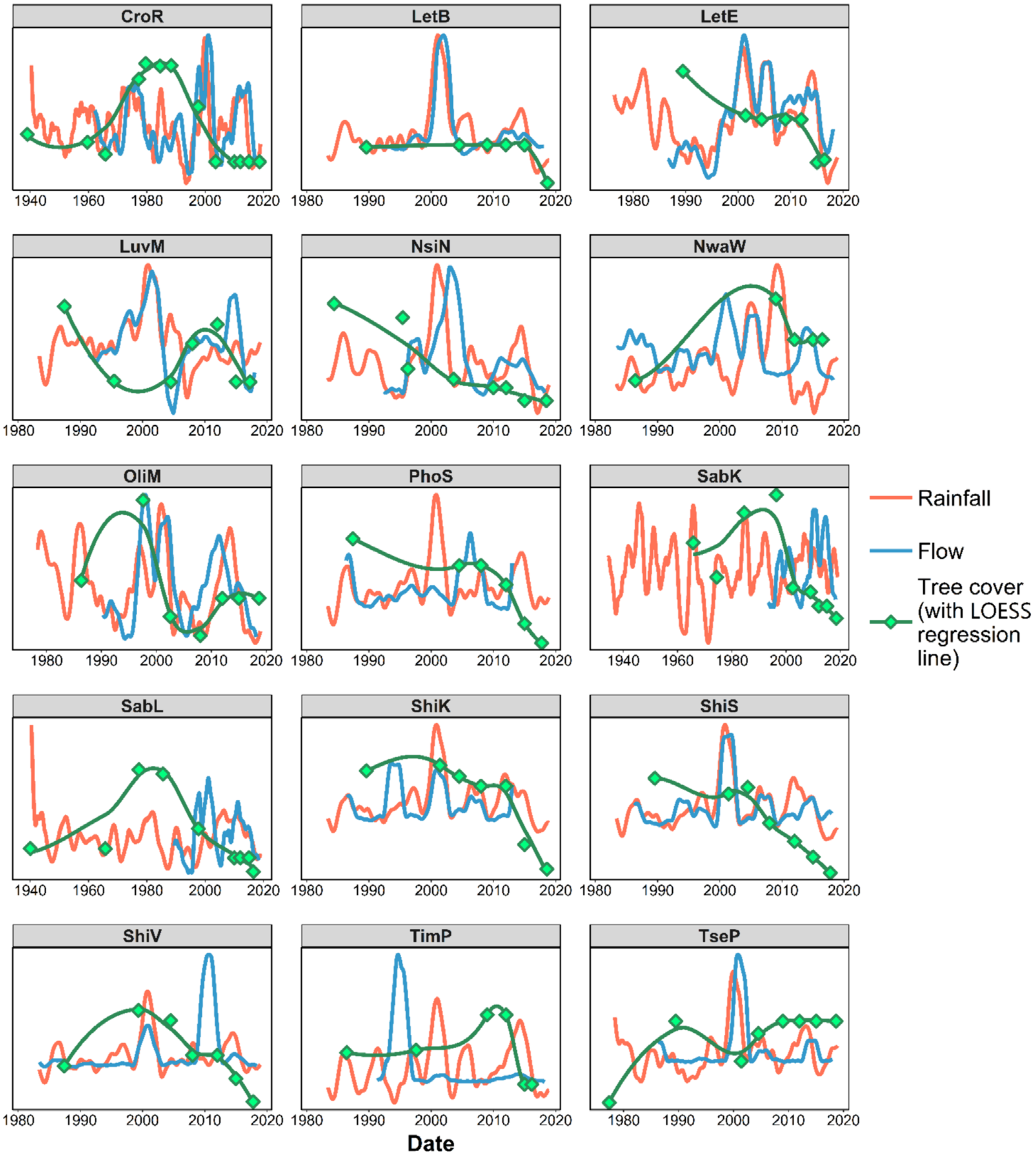

FIGURE 7 Trends in tree cover, deseasonalised rainfall and deseasonalised river flow at each study site. Smooth moving average lines were used for rainfall and flow. A LOESS regression curve was fitted to tree cover data to show trends at each site. Three sites excluded were OliB for the low flow data availability and reliability, CroT due to zero values for tree cover and BiyM due to the minimal overlap of the three variables. Data were scaled to ensure fit on one graph, and thus, scale does not represent actual values.

TABLE 2 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. Coefficients have been multiplied by 1000.

Response variable	Explanatory variable	Coefficient × 10^3 (mean change)	Std. error × 10^3	*T* value	*P* value
Tree cover change (proportional)	Maximum flow recorded (event)	≈−1.0	<0.1	−2.000	0.049
	CV flow	7.0	3.3	2.157	0.034
	Cumulative rainfall	≈0.1	<0.1	1.996	0.049
	Maximum monthly rainfall recorded	−0.5	0.1	−2.560	0.012

sites with greater tree cover showed greater declines in vegetation, likely because there are simply more trees vulnerable to damage, die-back 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 (Marnewick et al., 2015; O'Connor, 2010; WRC, 2001). 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 (O'Connor, 2001, 2010; Viljoen, 1995). In contrast to drought, floods are strongly episodic causing rapid changes and especially through the physical removal of trees (Naiman & Decamps, 1997). Our study corresponds to this in that the maximum flow (peak flood events) recorded and maximum monthly rainfall recorded were statistically significant in explaining proportional tree cover loss across all sites.

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 periods of high rainfall CV broadly coincided with losses in vegetation. This indicates that riparian areas benefit from more consistent rainfall. However, 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 (Fitchett, 2018; van Wilgen et al., 2016), mean 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.

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. Ecotones comprising habitats adjacent to non-perennial rivers may warrant more research and management focus in order to meet biodiversity conservation goals considering the generally reduced impact of large infrequent disturbances on riparian woodlands along the non-perennial rivers in this study and given the impacts of climate change on these systems and their responses and resilience (Kark, 2013). The quandary that arises is that riparian and river research requires long-term study (O'Connor, 2010), 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 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 that remove riparian vegetation are likely to make riverine areas more susceptible to subsequent floods through lower buffering capacity as hydrographic attenuation is lost. Further, it is likely that other factors, particularly herbivory (driven mostly by elephants) and fire, both important variables in determining riparian vegetation woodland structure, 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 that should be considered in the wider view of these habitats (e.g., wind, age, creepers, lightning and insect herbivory; O'Connor, 2010). Unravelling the complexity of spatio-temporal change requires an approach combining remotely sensed time series analyses (at broader scales for older imagery with poor resolution this study) with more recent high-resolution imagery that allows structure and possibly individuals to be tracked over time (e.g., Brandt et al., 2020; Reiner et al., 2023) with repeated ground-based population monitoring that assess adult mortality and recruitment (e.g., Andersen, 2015; O'Connor; Swemmer et al., 2023).

5 | CONCLUSION AND CONSERVATION IMPLICATIONS

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 and thus has implications on for many taxa, the KNP and its mandate, and areas downstream in Mozambique. 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. In that vein, the riverine networks in KNP play an outsized role in visitation by tourists (Turpie & Joubert, 2001).

The park seeks to promote adaptive management that enhances heterogeneity and thus flux in systems. The persistence of large trees is vital in savanna ecosystems, 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 upstream landowners to ensure catchment-wide strategies that promote and ensure environmental water requirement flows in accordance with legislation and for biodiversity maintenance if it is within their resource allocation.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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