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Rapid Establishment and Impact Assessment of the Redclaw Crayfish (*Cherax quadricarinatus*) Invasion in the Kruger National Park, South Africa

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ABSTRACT

Amidst the rapid degradation of the environment, protected areas act as a buffer for sensitive species against drivers of change. The Kruger National Park, in the Zambezian Lowveld Freshwater Ecoregion, encompasses two critical transboundary river basins, which are threatened by overexploitation, climate change and nonnative invasive species. We complete an assessment of the abundance, distribution, spread and potential impacts of the invasive redclaw crayfish on community assemblages throughout the five main rivers of the Kruger National Park and compare them to other invasive populations in Southern Africa. Redclaw crayfish have established populations in the Crocodile River and the Sabie-Sand River and are spreading at a rate of 7–8 km/year downstream and 3 km/year upstream. Abundance is lower than the more established invasions, but based on other trajectories, we can expect a tenfold increase in the next 5 years. No impact of crayfish presence or abundance was detected on fish or macroinvertebrate community assemblages. This suggests that as crayfish abundance is still relatively low, there may be a window of opportunity for targeted management. Management options in the rivers of the Kruger National Park are fraught with practical issues due to dangerous megafauna, but further understanding of the role of environmental flows on the establishment capacity of redclaw crayfish may hold some potential. Preventing new incursions into the protected area from watersheds originating outside of the park will need strategic multiorganisational collaboration.

1 | Introduction

During an era of rapid environmental change and biodiversity loss, especially pronounced in freshwaters, the role of protected areas in conserving aquatic ecosystems is imperative (Acreman et al. 2020; Tickner et al. 2020). Protected areas, including National Parks, must ensure persistent, healthy ecosystem functioning from disruption by major threats of

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overexploitation, pollution, climate change, habitat destruction and biological invasions (Acreman et al. 2020; dos Santos Mollmann et al. 2022). The Convention on Biological Diversity identified 20 Aichi Targets, including Target 11, which focuses on conserving at least 17% of global inland water areas through effectively and equitably managed, ecologically representative and well-connected systems of protected areas (Juffe-Bignoli et al. 2016). Maintaining a biodiverse and naturally functioning ecosystem may provide a buffer against the negative impacts of multiple synergistic stressors (Mungi et al. 2021; Gillingham et al. 2024). Historically, protected areas have not explicitly accounted for freshwater biodiversity during planning and implementation stages, with large, often transboundary rivers being used to delineate park borders (Roux et al. 2008). A difficulty in protecting both terrestrial and river ecosystems is that it is often impossible to protect rivers from source to sea, and if the middle and lower reaches of rivers are protected, upstream sources often impact protected downstream reaches of rivers (Burnett et al. 2022). The freshwater component of protected areas can also act as a conduit for stressors originating outside or adjacent to protected areas (e.g., invasive species and sources of upstream pollution) to enter and counteract conservation efforts (dos Santos Mollmann et al. 2022). Funding for conservation initiatives is often very thinly spread, especially for freshwater conservation, and management efforts need to be allocated carefully to maximise potential benefit (Watson et al. 2014).

Invasive nonnative species (*sensu* Soto et al. 2024) can cause severe negative impacts across all levels of biological organisation within protected areas, thus warranting high monetary investment in management (Ziller et al. 2020; Moodley et al. 2022; Carneiro et al. 2024). Despite biological invasions being solely responsible for 16% of extinctions and incurring enormous economic burden (IPBES 2023), management of aquatic ecosystems in protected areas is invested in the least, while also acting as an untapped invasion pathway from nonprotected upstream reaches (Moodley et al. 2022). To address the threats from biological invasions in protected areas, a strong understanding of invasion status, distribution, abundance and ecological impacts is critical to direct resources appropriately across a landscape.

Freshwater crayfish are prolific and successful invasive species worldwide due to their high generalism in feeding and habitat use; rapid reproduction rates, growth and fast maturing; large hard-shelled bodies; and predation defence attributes (Gherardi 2007; van Kuijk et al. 2021; O'Hea Miller et al. 2024). They have been introduced through both the ornamental trade pathway (Barkhuizen et al. 2022; Olden and Carvalho 2024) and through aquaculture ventures (Madzivanzira et al. 2020; Haubrock et al. 2021). The ecological and economic impacts of crayfish invasions are generally acknowledged to be high, largely due to polytrophic feeding attributes, meaning every level of the food web may be affected alongside transfer of pathogens (Lodge et al. 2012; Du Preez and Smit 2013; Twardochleb et al. 2013; O'Hea Miller et al. 2024). Furthermore, shredding behaviour may drive shifts in nutrient availability as well as physically changing ecosystem conditions (Lodge et al. 2012; Twardochleb et al. 2013). Globally, management costs associated with freshwater crayfish invasions are estimated to be at least US$5.7 million a year (Kouba et al. 2022).

Continental Africa has no native crayfish species, thus making them phenotypically novel in the African freshwater assemblage. Freshwater crabs (*Potamonautes* spp.) are the only functionally analogous decapod present in African systems, which are generally devoid of large-bodied shredder species. The niche similarity hypothesis suggests that when invasive species occupy the same functional niche as a native species, the native species will be threatened or outcompeted, or alternatively, as crayfish do not have an eco-evolutionary history in Africa, they may be filling an empty niche and not exerting pressure on the native assemblages (Herbold and Moyle 1986; Lodge et al. 2012; Daly et al. 2023). A particular species of concern is the emerging global invader, the redclaw crayfish (*Cherax quadricarinatus*), populations of which are now established through ecologically and economically important African water bodies in Zambia, Zimbabwe, South Africa, eSwatini and Mozambique (Nunes, Zengeya, Hoffman, et al. 2017; Nunes, Zengeya, Measey, et al. 2017; Douthwaite et al. 2018; Madzivanzira et al. 2021a; Haubrock et al. 2021; Ion et al. 2024). Native to northern Australia and Papua New Guinea, in its invasive range, the redclaw crayfish can exert predatory pressure on fish, molluscs and macrophytes and compete with native species such as freshwater crabs and shrimps for food and shelter (Marufu et al. 2018; Zeng et al. 2019; Madzivanzira et al. 2021b, 2022; Zengeya et al. 2022; Baudry et al. 2024a, 2024b). In addition, there is evidence of socioeconomic impacts conferred through extreme monetary loss to fisheries through their scavenging behaviour (Madzivanzira et al. 2022, 2023; Chakandinakira et al. 2023). Crayfish may also pose a human health risk if consumed, as they bioaccumulate heavy metals (Erasmus et al. 2024).

The Kruger National Park (KNP) is a flagship protected area in South Africa, bordered by Mozambique and Zimbabwe at the northern and eastern limits of the park, which is further encompassed by a mosaic of private game reserves and transfrontier/transboundary reserves in Botswana, Zimbabwe and Mozambique that collectively make up the Greater Limpopo Transfrontier Park (GLTP). Two major transboundary river basins (Limpopo and Inkomati) encompass the parks freshwater ecosystems, all of which fall within the highly biodiverse Zambezian Lowveld ecoregion (Abell et al. 2008; Chakona et al. 2022; Ntokoane et al. 2025). Within the KNP and larger GLTP, there are at least two endangered fishes (*Serranochromis meridianus* and *Chetia brevis*) and two critically endangered fishes (*Chiloglanis bifurcus* and *Enteromius treurensis*), although both *E. treurensis* and *C. bifurcus* have not been sampled more than once within the KNP (FBIS 2022, accessed 2025). Both the Limpopo and Inkomati basins have been invaded by redclaw crayfish. The Inkomati invasion vector was an aquaculture escape from the flooding of a facility on the Sand River Dam in eSwatini, whereas the origin of the Limpopo invasion is uncertain, with the first record of invasion in the South African portion of the Komati River in 2002 (de Villiers 2015; Nunes, Zengeya, Hoffman, et al. 2017; Madzivanzira et al. 2020). Redclaw crayfish were first reported as present in low abundance in the Crocodile River below Van Graan Dam on the border of KNP in February 2016 (Petersen et al. 2017). The presence of redclaw crayfish has been informally described since 2022 in the northern tributaries of the Inkomati Basin in the Sand River and in the lower reaches of the basin in the Incomati River Floodplain

(G. O'Brien, unpublished data). Although numerous calls for early action and further assessment of threats posed by redclaw crayfish to KNP have been made (e.g., Petersen et al. 2017; Nunes, Zengeya, Hoffman, et al. 2017; Nunes, Zengeya, Measey, et al. 2017; Madzivanzira et al. 2020, 2021a), until now, there has been no conservation action.

To address the information gap hindering proactive conservation action, we completed a large-scale survey of the five main rivers of the KNP to assess redclaw crayfish distribution and abundance, invasion dynamics, selection processes acting on the population and ecological impact on the fish and macroinvertebrate communities. The redclaw crayfish invasions in southern Africa have all been surveyed with a standardised methodology developed for the region (see Madzivanzira et al. 2021c). We are therefore able to compare invasion trajectories both spatially and temporally against the other invasion cores in the Komati River in the Zambezian Lowveld ecoregion (Nunes, Zengeya, Hoffman, et al. 2017), Kafue Floodplains ecoregion (Madzivanzira et al. 2021a), the Upper Zambezi Floodplains ecoregion (Madzivanzira et al. 2021a; Nawa et al. 2024) and Lake Kariba in the Middle Zambezi-Luangwa ecoregion (Madzivanzira et al. 2021a). Nawa et al. (2024) reported signals of spatial sorting on the invasive population in the Barotse floodplain, Zambia, where individuals were longer legged at the edges of the invasive range. It was therefore hypothesised that longer legs may be related to improved dispersal ability in the drying-wetting regime of the floodplain. Thus, we also measured leg length and compared our measurements across the KNP invasion gradient to understand selection of dispersal processes. Limited field studies have been completed to assess the ecological impacts of redclaw crayfish on trophic analogues, fish and macroinvertebrate assemblages; therefore, we aimed to assess these impacts in the KNP. This rapid assessment can be used to guide future hotspots for proactive control measures and biodiversity monitoring in line with the South African National Parks' (SANParks) conservation policy (eradicate invasive species in protected areas) and the maintenance of heritage assets and thereby providing human benefits (National Environmental Management Biodiversity Act [NEM:BA 10 of 2004]; SANParks 2024).

2 | Methods

2.1 | Study Area

The KNP is in the lowveld savannah, South Africa, and covers an approximate area of 19,500 km^2 (Figure 1a). The KNP is South Africa's most downstream 'water user' of the five major perennial transboundary east flowing rivers of southern Africa that flow from South Africa, between Zimbabwe (Limpopo River) and all

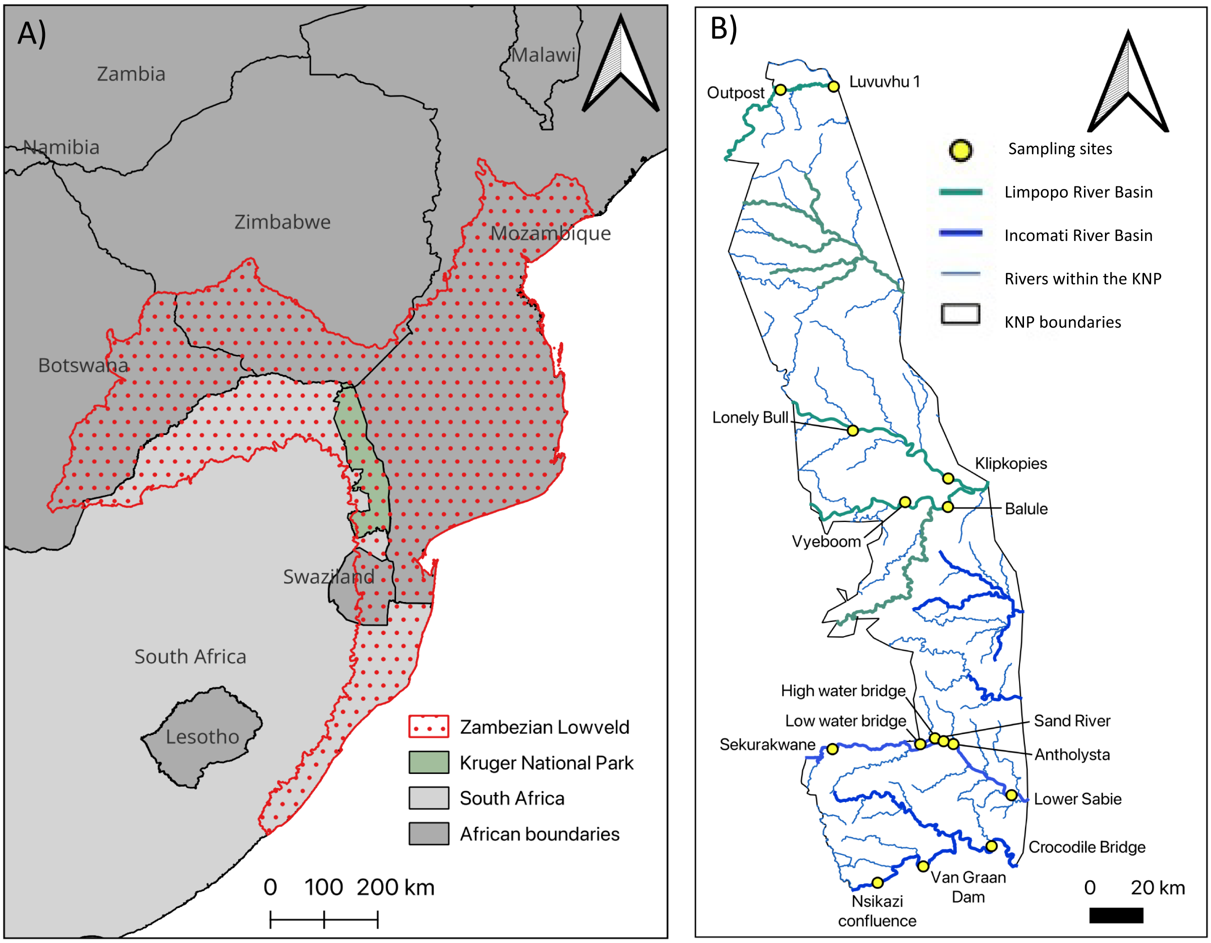

FIGURE 1 | (A) Map of the Kruger National Park (KNP), South Africa, situated within the Zambezian Lowveld ecoregion and (B) distribution of sampling sites on the rivers of KNP.

into Mozambique (i.e., KNP forms the South African limits of each river) (Pollard et al. 2011). The rivers are all in the region's subtropical climate and exhibit a highly variable flow associated with variable rainfall distribution along a gradient of increasing rainfall from north (500–600 mm per year) to south (700–800 mm per year) (MacFadyen et al. 2018). The perennial rivers of the KNP are found within two river basins, that is, Limpopo (Luvuvhu, Letaba and Olifants Rivers) and Inkomati (Sabie, Sand and Crocodile Rivers) (Figure 1b), and are characterised by different land use practices along the river gradient (Roux et al. 2008). The entire KNP, as the core of the GLTP, falls within the Zambezian Lowveld aquatic ecoregion (ID 576 per Abell et al. 2008), which includes easterly flowing alluvial terraced rivers and low-level coastal plain river reaches. The ecoregion includes numerous freshwater habitats from subtropical and tropical coastal rivers as a part of the large Limpopo and Inkomati river basins and ephemeral pans (Skelton 2001). The Zambezian Lowveld ecoregion supports the highest fish diversity in South Africa with > 67 freshwater fish species identified thus far (Chakona et al. 2022; Ntokoane et al. 2025), out of an approximate 100 species found within South Africa, and a total of 105 species within the ecoregion itself (Roux et al. 2023). The Komati Primary Catchment holds the second highest number of threatened freshwater fishes in South Africa and therefore considerable conservation value (Kajee et al. 2023). Beyond aquatic biodiversity, KNP is South Africa's biggest protected area, encompassing ~5% of the country's land mass (Roux et al. 2008), where all terrestrial biodiversity is inherently supported by the integrity of the freshwater systems.

The KNP has a long history of biological invasions and management of such, having been invaded by many terrestrial plants (e.g., famine weed *Parthenium hysterophorus* and *Lantana camara*), floating macrophytes (e.g., water hyacinth *Pontederia crassipes* and water lettuce *Pistia stratiotes*), gastropods (e.g., quilted melania *Tarebia granifera*) and fish (e.g., silver carp *Hypophthalmichthys molitrix* and Nile tilapia *Oreochromis niloticus*) (Macdonald 1988; Crookes et al. 2020; FBIS 2022). The redclaw crayfish represents the first crustacean invasion of the park (Petersen et al. 2017).

2.2 | Sampling

All work was completed under KNP Permit Number and Ethical Approval SS1413.

2.2.1 | Crayfish

Sampling took place in July 2024, covering 16 sites distributed across the Crocodile (3), Sabie—including three sites on its major tributary the Sand River (7), Olifants (2), Letaba (2) and Luvuvhu (2) rivers with a total of 382 trap nights (Figure 1b). We followed the standardised method for sampling redclaw crayfish in southern Africa (Madzivanzira et al. 2021c), where Promar collapsible crayfish traps (dimensions: 61 × 46 × 20 cm; mesh size: 10 mm) were deployed with ~100-g dry dog food as bait. Traps were deployed at least 10 m apart, in the afternoons, and left overnight for around a 15 h soak time. When retrieved, the number of crayfish caught in each trap was recorded, including whether females were berried or ovigerous. Morphometric measurements were taken for each individual: carapace length (CL), carapace width (CW), front leg length (FLL), chelae length (ClL), mass (g) and sexed (male, female, intersex or juvenile if too small) (Madzivanzira et al. 2021a; Nawa et al. 2024). Any crabs caught in the traps were recorded for the same measurements apart from FLL (Data S1). All fish bycatch was identified to species level, and the number was recorded (Data S1).

2.2.2 | Community Assemblages

Fish assemblages were sampled using a backpack SUM electrofisher, with a 5-mm mesh scoop net in wadable reaches. All habitat types were sampled exhaustively until no more new species were caught. Due to the presence of dangerous megafauna, deep pools were not able to be sampled. Species presence–absence was recorded, and any crayfish caught during the electrofishing passes were kept for morphometric measurements (Data S1 and S2).

Macroinvertebrate communities were sampled following the South African Scoring System (SASS5) per Dickens and Graham (2002). This involves standardised search procedures (kicking, sweeping hand searching) in each biotope present. Species were then identified to family level and recorded for presence/absence (Data S1).

All sites were sampled for fish and macroinvertebrates apart from the three Sand River sites and at site Luvuvhu 1 + 2 due to either time constraints or safety concerns. Temperature and dissolved oxygen were measured at all sites apart from in the Sand River due to equipment malfunction. All animals were released on site apart from invasive non-native species (per NEM:BA 10 of 2004; SANParks 2024).

2.3 | Data Analysis

All analysis was completed in R 4.4.2 (2024-10-31).

2.3.1 | Crayfish Distribution and Abundance in the KNP

Trap efficiency was assessed using detection probability (PC) and was expressed as the proportion of traps containing at least one crayfish. Catch per unit effort (CPUE) was used as a proxy for relative abundance, that is, crayfish caught per trap per night. Due to only four sites having detected crayfish in traps, it was not possible to compare PC and CPUE values between rivers within the KNP. To centre this new invasion core in the context of the other in southern African redclaw crayfish invasions, we compiled the raw data from three published surveys using the standardised sampling protocol (per Madzivanzira et al. 2021c) to compare CPUE and PC from the invasion in the KNP to other locations with known introduction dates (Table 2 and Data S2), although it was not possible to derive values for PC from Nunes, Zengeya, Hoffman, et al. (2017). Kruskal–Wallis tests were used for all variables, and differences were addressed post hoc using a Wilcoxon signed rank test with Holm–Bonferroni corrections for multiple comparisons due to nonequal variances across groups and nonnormal distributions. All data from the

KNP were treated as one invasion core for this purpose. We report only the differences between KNP and other invasions, but full comparisons can be found in the R code in the Supporting Information. All data are deposited in the World of Crayfish repository (Ion et al. 2024).

2.3.2 | Invasion Dynamics

Minimum invaded river length and spread rate was calculated in QGIS v. 3.30.2 by snapping each trap location to the National Freshwater Ecosystem Priority Areas (NFEPA) river network shapefile using the Snap Geometries to Layer tool (tolerance = 10 m) and then calculating the Shortest Path (Point to Point) in the Network Analysis toolbox, along the river network from the uppermost and lower most trap where crayfish were present on each river. The Van Graan Dam (Crocodile River) and low water bridge (Sand River tributary of the Sabie River) were considered as the invasion core. Distances were then divided by the number of years since detection—8 years in the Crocodile River (Petersen et al. 2017) and 2 years in the Sabie-Sand (G. O'Brien, unpublished data). Distance from core was recorded for each trap locality.

We calculated differences in sex ratio across the sampling sites in the KNP using a 3×4 contingency table, and across the six invasion cores using a 3×6 contingency table, with a χ^2 test of independence, excluding unsexed juveniles.

The compiled data from the other southern African invasion cores (Table 1 and Data S2) were used to compare CL and mass ranges from the KNP following the same statistical analysis described above for CPUE and PC.

2.3.3 | Selection Processes

To assess whether spatial sorting is acting on the population in the KNP invasion gradient regarding FLL, we regressed FLL values against CL with a linear model and used the residuals in a second linear regression against distance from the introduction point. As the introduction point was not known for the Sabie-Sand invasion, we took the coordinates of the site with the highest CPUE (i.e., low water bridge) as the invasion core. Due to low sample size and sex-based differences in chelae morphology, we were not able to test whether there was weapons' investment at the invasion front per Nawa et al. (2024); sex was excluded as a factor in the analysis for FLL.

2.3.4 | Ecological Impact

A binomial GLM with a logit link function and analysis of deviance tables via the R package ‘car’ (Fox and Weisberg 2018) was used to determine whether the presence of crayfish in traps reduces the likelihood of freshwater crab presence in the system. To do this, we used the compiled dataset from invasion cores, which had crab presence–absence recorded in individual traps, in combination with new data from the present study, resulting in a dataset from Kafue floodplains, Barotse floodplains and KNP (Data S3). No crabs were caught during sampling of Lake Kariba, so this was excluded from analysis.

The R package ‘vegan’ (Oksanen et al. 2019) was used to first check sampling efficiency using *vegan::specaccum*; then, analysis of variance was used to test whether sites with crayfish present differ in species richness. This analysis excluded sites sand, low water bridge, high water bridge and Luvuvhu 1 + 2. Then, non-metric multidimensional scaling plots were constructed using *vegan:metaMDS* with Jaccard dissimilarity based on presence/absence for both the fish and macroinvertebrate assemblage due to semiquantitative estimates of abundance. Environmental variables, crayfish abundance, crayfish presence/absence, dissolved oxygen, temperature and latitude were fitted to the data using *vegan::envfit*. After checking for homogeneity of variance using *vegan::betadisper*, PERMANOVA tests were used to determine whether macroinvertebrate and fish communities differed between invaded and uninvaded sites using a Jaccard dissimilarity matrix and 999 permutations. A MANTEL test with a single fixed effect of crayfish relative abundance (CPUE) on

TABLE 1 | Southern African redclaw crayfish (*Cherax quadricarinatus*) invasion cores sampled using standardised methodology.

Invasion core	Sampling year	Introduction year	Time since invasion (years)	PC	CPUE	Study
Barotse floodplain	2019	2014	5	0.56	2.34 ± 3.25	Madzivanzira et al. (2021a)
Barotse floodplain	2021	2014	7	0.29	1.20 ± 2.16	Nawa et al. (2024)
Kafue floodplains	2017	2001	16	0.65	5.11 ± 7.79	Madzivanzira et al. (2021a)
Lake Kariba	2018	2002	16	0.65	4.41 ± 3.50	Madzivanzira et al. (2021a)
Komati River	2016	2002	14		2.44 ± 2.93	Nunes, Zengeya, Hoffman, et al. (2017)
Kruger National Park	2024	2016	8	0.11	0.16 ± 0.13	South et al. (present study)

a Manhattan distance matrix was used to ascertain whether crayfish abundance was related to macroinvertebrate and fish community structure using Spearman's correlation and 999 permutations, again on the Jaccard dissimilarity matrix for each community dataset.

3 | Results

3.1 | Crayfish Distribution and Abundance in the KNP

A total of 382 traps were set, and 378 were collected, with some loss attributed to controlled water releases upstream and megafauna (e.g., crocodiles [*Crocodylus niloticus*], hippopotamus [*Hippopotamus amphibius*] and elephants [*Loxodonta africana*]) dislodging them. Crayfish were detected in the Crocodile River; the Sand River, which is a major tributary of the Sabie River; and the mainstem of the Sabie River (Figure 2). Besides redclaw crayfish, here, we also note the presence of one nonnative invasive largemouth bass (*Micropterus nigricans*) at Sekurakwane, caught while electrofishing (standard length 130 mm).

A total of 24 crayfish were caught across four sites with the traps, and six were caught during electrofishing (Table 3). At one site, Nsikazi Confluence, four crayfish were caught by electrofishing, but no crayfish were caught in the traps; thus, crayfish were present at 100% of sampled sites in the Crocodile River (Table 2). While electrofishing directly below Van Graan Dam, many crayfish were observed but unable to be captured due to the seasonal filamentous algae at the site. In the four sites where crayfish were caught in traps, the PC ranged from 0.04 to 0.18, and the CPUE ranged from 0.04 to 0.35 ind./trap/night (Table 2 and Figure 2).

There were significant differences in CPUE across the southern African invasion cores (Kruskal–Wallis $\chi^2 = 36.585$, $df = 5$, p value < 0.001), whereby the CPUE in the KNP was lower than that of the Kafue, Kariba, Komati and Barotse 2019 invasion cores (all $p < 0.05$; Table 2 and Figure 3). Values of PC were significantly different (Kruskal–Wallis $\chi^2 = 23.593$, $df = 4$, p value < 0.001; Tables 1 and 2 and Figure 3), where KNP PC was lower than Kariba ($p < 0.05$; Tables 1 and 2 and Figure 3) but comparable to the other locations (all $p < 0.01$; Tables 1 and 2 and Figure 3).

3.2 | Invasion Dynamics

River network lengths of invaded portions of the Crocodile River were 51.06 km from Van Graan Dam to Crocodile Bridge, where redclaw crayfish abundance was at trap detection probability and 81.36 km when considering individual crayfish detected via electrofishing at Nsikazi confluence. Using 2016 as the year of *C. quadricarinatus* first detection in the Crocodile River at Van Graan Dam (per Petersen et al. 2017), the downstream spread rate is estimated to be 6.38 km/year, and the upstream spread rate is 3.78 km/year. In the Sabie-Sand, redclaw

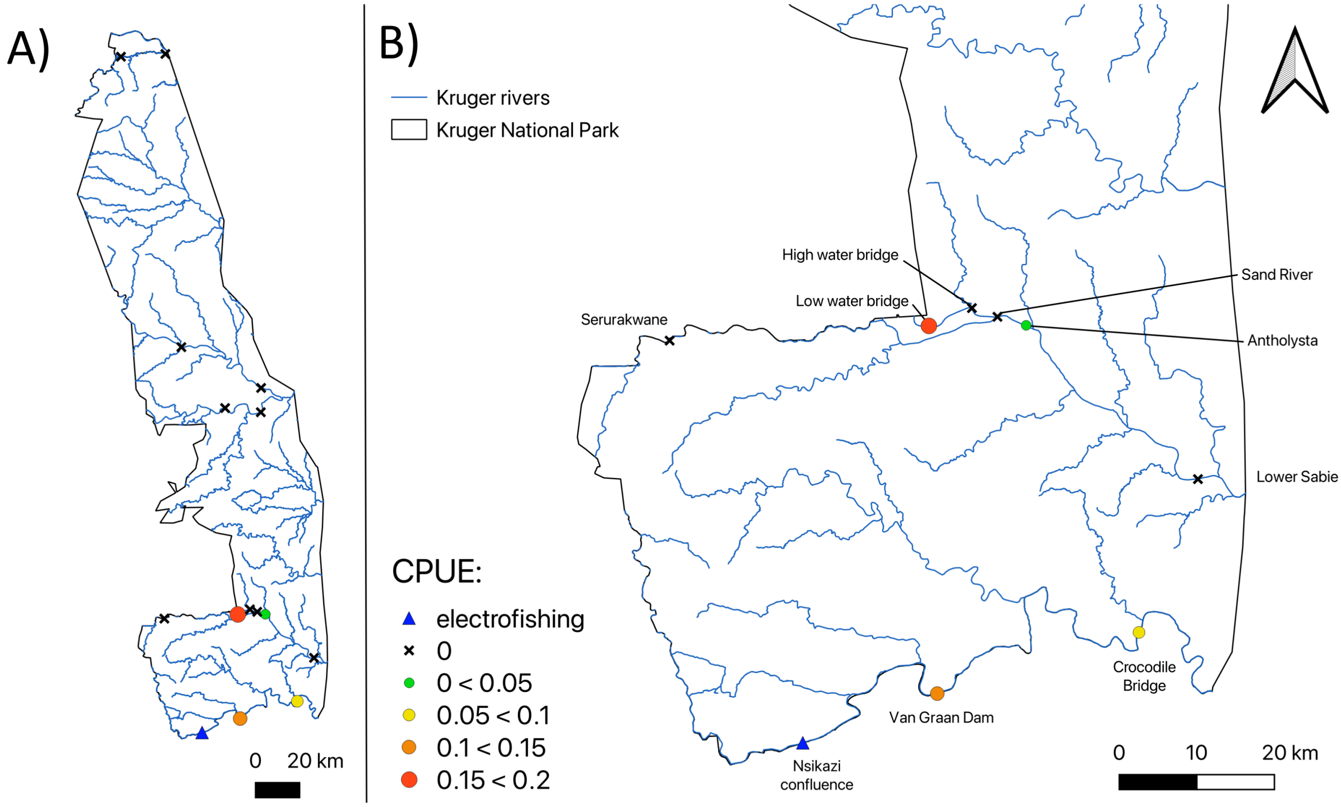

FIGURE 2 | (A) Relative abundance and spatial distribution of invasive redclaw crayfish (*Cherax quadricarinatus*) in sampling sites within the Kruger National Park from trapping and (B) spatial distribution of the invasion in just the invaded Crocodile and Sabie Rivers. Catch per unit effort (CPUE) is represented by coloured circles, and absence of crayfish is represented by black crosses; presence of crayfish detected by electrofishing but not trapping is indicated at one site (Nsikazi confluence) by a blue triangle.

TABLE 2 | Breakdown of trapping campaign for each site, including effort, crayfish catch per unit effort (CPUE), crayfish presence/absence accounting for crayfish caught by electrofishing but not trapping, detection probability (PC), fish species richness, macroinvertebrate family richness, temperature and dissolved oxygen.

River	Site	Effort (No. of traps/night)	Crayfish CPUE	Crayfish presence/absence	PC	Fish species richness	Macroinvertebrate family richness	Temperature (°C)	Dissolved oxygen (mg/L)
Sabie	Antholysta	24	0.042	Yes	0.04	17	24	20.4	8.75
Olifants	Balule	20	0	No		11	16	12.65	9.995
Crocodile	Crocodile Bridge	32	0.094	Yes	0.09	8	20	18.3	9.905
Sabie-Sand	High Water Bridge	3	0	No		—	—	—	—
Letaba	Klipkoppies	26	0	No		9	25	17.3	9.64
Letaba	Lonelybull	24	0	No		9	15	14.555	9.045
Sabie-Sand	Low Water Bridge	30	2	Yes	0.18				
Sabie	Lower Sabie	11	0	No		7	25	18.2	8.295
Luvhuvhu	Luvuvhu 1 + 2	29	0	No		—	—	20.33	9.19
Crocodile	Nsikazi Confluence	30	0	Yes		6	20	19.35	9.545
Luvhuvhu	Outpost	29	0	No		16	30	15.15	9.73
Sabie-Sand	Sand	12	0	No				—	
Sabie	Sekurakwane	31	0	No		19	20	14.4	9.45
Crocodile	Van Graan	46	0.522	Yes	0.13	12	21	17.95	8.065
Olifants	Vyeboom	30	0	No		7	14	19.3	9.92

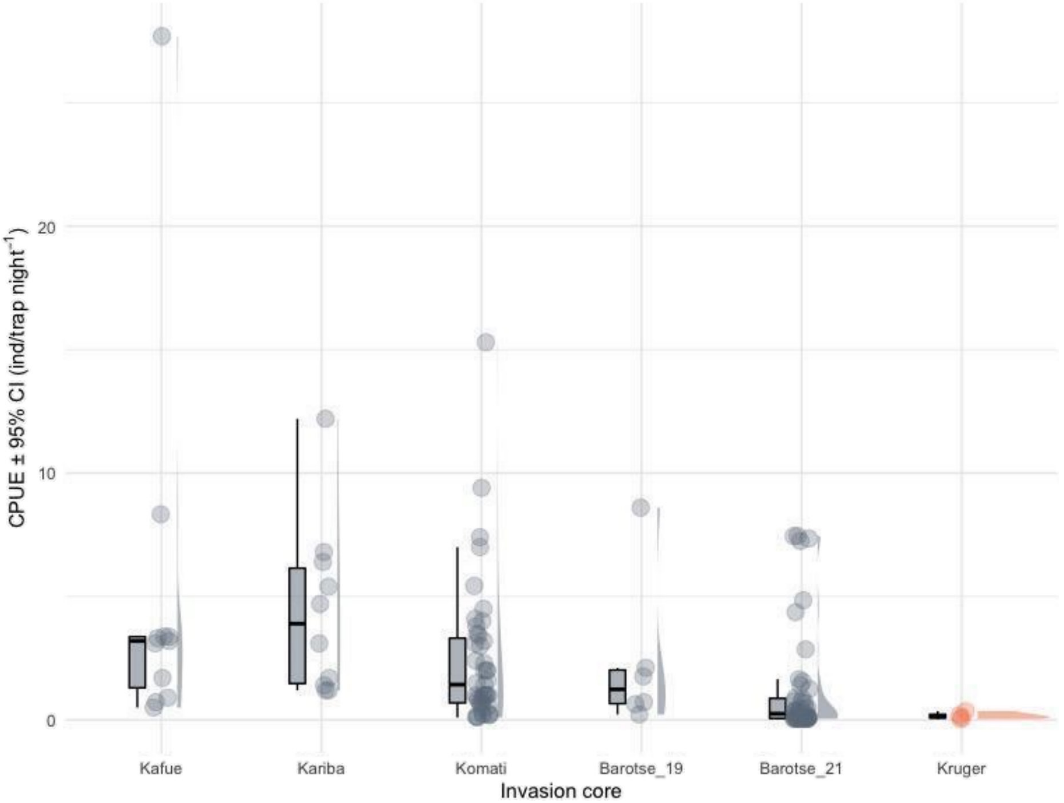

FIGURE 3 | Catch per unit effort (CPUE) of southern African redclaw crayfish (*Cherax quadricarinatus*) invasion cores with boxplots, indicating median and interquartile ranges and individual points representing CPUE at each sampling site. Data for the Kafue, Kariba and Barotse_19 from Madzivanzira et al. (2021a), Komati from Nunes, Zengeya, Hoffman, et al. (2017), Barotse_21 from Nawa et al. (2024) in grey, and Kruger National Park from the present study in coral. All raw data can be found in Data S2.

crayfish are present in at least 14.8 km of river from the Low Water bridge in the Sand River to the Antholysta site in the Sabie River (Figure 2a,b). Using 2022 as the year of first detection (G. O'Brien, unpublished dat), and taking the low water bridge site as an introduction site, the downstream spread rate in the Sabie-Sand is estimated at 7.4 km/year.

This study comprised 59% females, 14% males and 5% intersex. Four juvenile specimens that could not be sexed (18%) were caught at one site, Nsikazi confluence, via electrofishing. The female:male:intersex ratio was 4:3:1, and there were no differences between the five invaded sites within the KNP ($\chi^2 = 8$, df = 6, $p = 0.23$) nor between the six invasion cores ($\chi^2 = 30$, df = 25, $p = 0.22$).

Carapace length (CL) and mass were significantly different across invasion cores (CL: $\chi^2 = 251.94$, df = 5, p value < 0.001; mass: $\chi^2 = 200.59$, df = 5, p value < 0.001; Figure 4a,b). The KNP population has significantly shorter CL and lower mass overall compared to the invasion cores in Kafue, Kariba and Barotse 2021 (all $p < 0.05$; Table 3) but comparable to both Barotse 2019 and Komati invasion cores.

3.3 | Selection Processes

There was no relationship between distance from the introduction point and FLL nor an effect of the river system ($R^2 = 0.03$, F [2, 20] = 0.34, $p = 0.71$).

3.4 | Ecological Impact

There was no effect of crayfish presence on the likelihood of detecting a freshwater crab in the same trap across all three invasion cores ($\beta = 0.81$, SE = 0.62, $z = 1.30$, $p = 0.19$).

There was no difference in fish or macroinvertebrate species richness between invaded and uninvaded sites (fish: $F = 0.73$, df = 3, $p = 0.56$; macroinvertebrates: $F = 0.02$, df = 1, $p = 0.87$; Table 2).

The nMDS stress values for both fish and macroinvertebrate assemblage ordination were < 0.2 and therefore appropriately displayed on two dimensions. None of the environmental parameters measured were significant in the nMDS fitting for fish or macroinvertebrates. Crayfish presence did not affect fish or macroinvertebrate communities (PERMANOVA; fish: pseudo-$F1,10 = 1.44$, $R^2 = 0.13$, p value = 0.18; macroinvertebrate: pseudo-$F1,10 = 0.55$, $R^2 = 0.05$, p value = 0.87; Figure 5a,b), and there was no effect of crayfish abundance on fish or macroinvertebrate community structure (MANTEL; fish: $R^2 = 0.25$, $p = 0.11$; macroinvertebrate: $R^2 = -0.09$, $p = 0.66$; Figure 5a,b).

4 | Discussion

Multiple established invasions of the redclaw crayfish have the potential to threaten the freshwater ecosystems of the KNP. We report on the extent of two newly detected invasions spreading

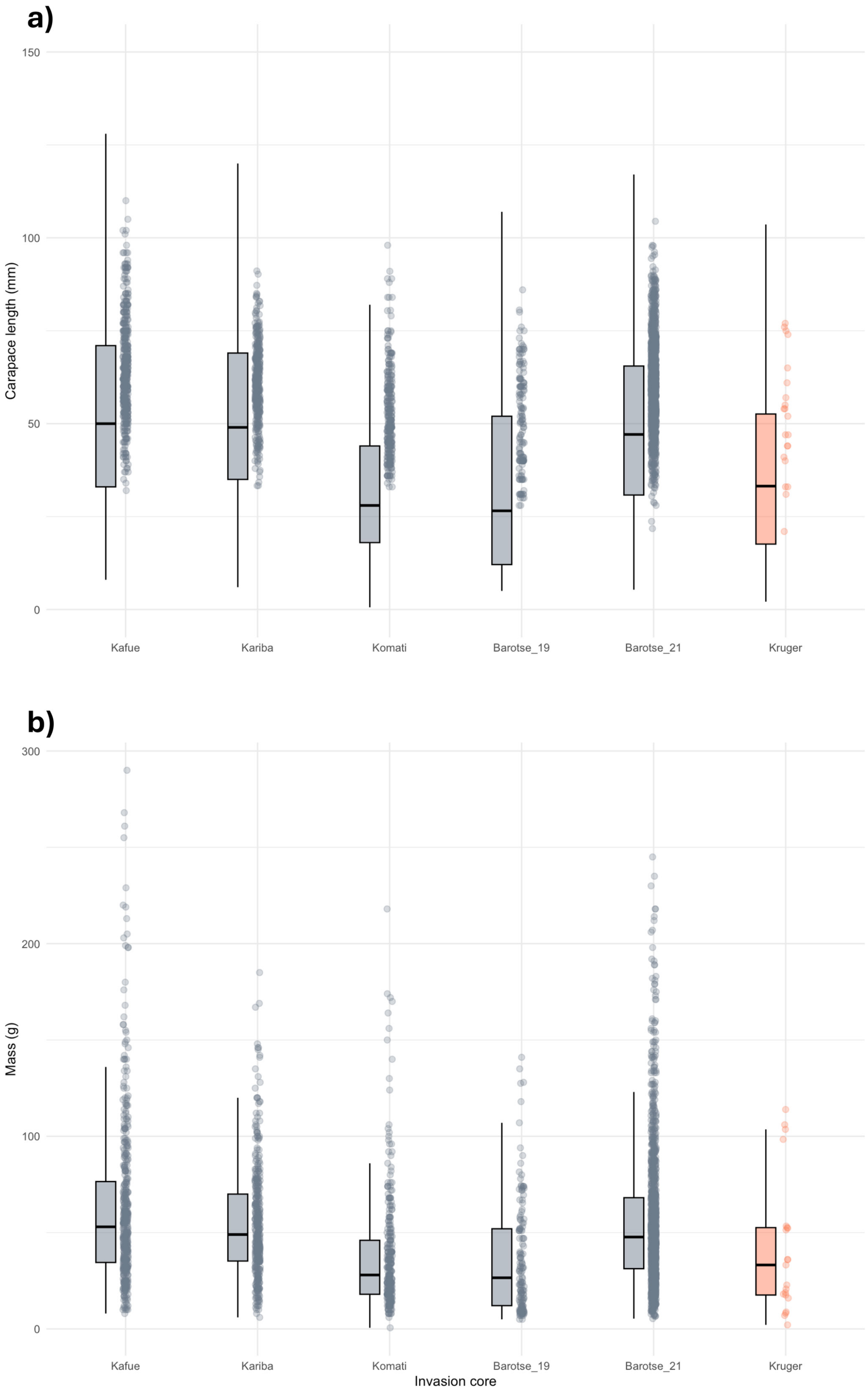

FIGURE 4 | (a) Carapace length (mm) and (b) mass (g) distributions of African redclaw crayfish (*Cherax quadricarinatus*) in southern African invasion cores with boxplots indicating median and interquartile ranges and individual points representing individual crayfish. Data for the Kafue, Kariba and Barotse_19 from Madzivanzira et al. (2021a), Komati from Nunes, Zengeya, Hoffman, et al. (2017), Barotse_21 from Nawa et al. (2024) in grey and KNP from the present study in coral. All raw data available in Data S2.

TABLE 3 | Number and morphometric values of crayfish caught by trapping and electrofishing in each site.

River	Site	Number of crayfish	CL	CW	ClL	FLL	Mass
Sabie	Antholysta	1	56 ± 12.7	25 ± 7.0	35.5 ± 16.3	41 ± 13.1	34.8 ± 23.5
Crocodile	Crocodile Bridge	3	60.7 ± 13.5	26.7 ± 7.51	43.3 ± 11.5	843 ± 8.72	59.9 ± 40.8
Sand	Low water bridge	2	53.1.4	20.5 ± 0.7	56	35 ± 1.41	36 ± 0
Crocodile	Nsikazi confluence	4	34.5 ± 10.1	13.8 ± 4.0	19.2 ± 9.11	22.5 ± 9.26	10.7 ± 7.38
Crocodile	Van Graan	12	54.3 ± 17.3	26.7 ± 7.5	40.4 ± 16.9	36.6 ± 11.9	51.3 ± 41

Abbreviations: CL, carapace length; ClL, chelae length; CW, carapace width; FLL, front leg length in mm and mass in g.

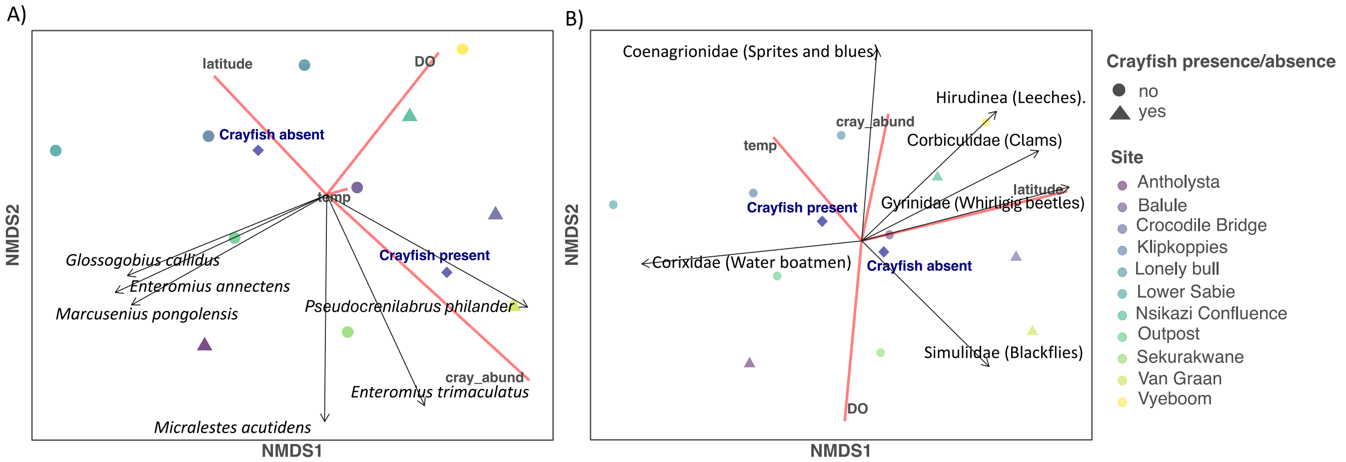

FIGURE 5 | nMDS ordination of (A) fish and (B) macroinvertebrate assemblages at 11 sampling sites in the Kruger National Park with relation to invasive redclaw crayfish (*Cherax quadricarinatus*) presence, which is indicated by triangles when present and circles for absent. Blue diamonds represent factor centroids. Vectors in red represent environmental variable loadings; thin grey lines represent significant loadings of intrinsic species/families based on *vegan::envfit*. Species and family presence absence matrices can be found in Data S1.

through the Crocodile and Sabie and Sand Rivers. The trajectory of invasion dynamics appears slower in comparison to locations, where redclaw crayfish have been established for a longer period in areas that are not protected, although initial invasion population dynamics in the Komati River were comparable in 2016 to other regional invasions. There were no signals of spatial sorting affecting dispersal traits in the population invading the KNP nor evidence of ecological impact at the community level in this first assessment. Relative abundance of redclaw crayfish is comparatively low within the protected area, which may be a result of biotic resistance, environmental factors such as the 5-year wet phase postdrought in the KNP or simply a facet of time since invasion; therefore, the lack of detectable impact at these levels of organisation should not be considered as absence of impact (Catford et al. 2022). Low abundance of crayfish indicates there may still be a window of opportunity to mitigate future ecological damage and associated costs to SANParks (Epanchin-Niell and Liebhold 2015; Cuthbert et al. 2022).

Two separate invasions by redclaw crayfish have been established in the Crocodile and Sabie Rivers, indicated by the presence of adults and juveniles in each population separated from each other across the basin. In both instances, the rivers originate from outside of the park and are part of the heavily invaded Incomati basin (Petersen et al. 2017; Nunes, Zengeya, Hoffman, et al. 2017). Therefore, the invasion pathway may be a mixture of both unhindered movement through the riverine corridor or due to illegal stocking of redclaw crayfish in the Mpumalanga Province. Determining invasion origin and connectivity between the Crocodile and Sabie River invasions should be a priority. Redclaw crayfish is a Category 1b invasive species according to South Africa's National Environmental Management: Biodiversity Act (NEM:BA) 10 (2004) regulations, meaning that possession, movement or selling of the species is prohibited. Public confusion may occur due to the recent NEM:BA delisting of another invasive crayfish species (*Procambarus clarkii*), thus potentially causing legislation misunderstanding, demotivating public concern relating to crayfish invasions and driving stakeholder conflict (Woodford et al. 2017; Barkhuizen et al. 2022). Targeted and clear biosecurity messages are needed to reduce human-mediated transportation between waterways. As the three rivers in the Limpopo catchment (Olifants, Letaba and Luvuvhu) are still free from redclaw crayfish, management efforts should be concentrated on controlling spread further north and restricting further spread within the Crocodile and Sabie Rivers. To do so would require coordination between SANParks and provincial environmental managers in both Limpopo and Mpumalanga to assess invasion extent in the freshwater bodies outside of the park. However, lack of financial capacity and a convoluted permitting system hinders completion of urgent baseline assessments needed for proactive management (Hamer et al. 2021). Reports of redclaw crayfish from the Ga-Selati River, which is near the confluence with the Olifants

River, were received in 2023, and samples were destroyed (D. Khosa, pers. obs). Thus, incursion into the northern rivers may have already started.

Using time since invasion and space for time substitutions can give insight into the trajectory of an invasion in its infancy and provide useful inferences in the absence of long-term temporal data within a site (Strayer et al. 2006; Catford et al. 2022). There were two clear invasion cores in both the Crocodile and the Sabie Rivers, but when compared to more established invasions, the relative abundance and PC in KNP were lower. This may be due to time since invasion, where invasion velocity generally follows a Pareto curve of rapid inflexion before plateauing (Strayer et al. 2006; Soto et al. 2023). Using the Komati River data (8 years) from Nunes, Zengeya, Hoffman, et al. (2017) as a space for time proxy in the same river basin, we could expect a tenfold increase in the relative abundance of crayfish in the next 5 years. Although when comparing invasions at similar time points to the KNP invasion (i.e., the Barotse floodplain; Madzivanzira et al. 2021a), the relative abundance in the Barotse is similar to the Komati, despite being a younger invasion. The Barotse floodplain is a 200-km floodplain of the upper Zambezi that mirrors the Australasian floodplain ecosystems that redclaw crayfish evolved in Barki et al. (2010). Therefore, the nondrying riverine systems of the Crocodile and Sabie Rivers may be a barrier to establishing high abundances but not colonisation, or the protected area of the KNP may be providing a buffer through biotic resistance (Macdonald 1988; Petruzzella et al. 2020). The Barotse floodplain, as sampled by Nawa et al. (2024) in 2021, encompasses both the core and the very front edge of the invasion; when subsetted into core and front, the CPUEs were 1.471 ± 0.685 and 0.027 ± 0.002 ind./trap/night, respectively. The CPUE at the Antholysta and Crocodile Bridge invasion fronts is similar to those from the Barotse floodplain, suggesting that these sites have been invaded and reached high enough abundance for trap detection probability within the last 2 years (Nawa et al. 2024).

Population and movement dynamics of redclaw crayfish in the KNP differ from the invasion cores in the Upper Zambezi but have some similarities to the wider Komati River invasion. Spread rate within the Crocodile River (6.38 km/year downstream and 3.78 km/year upstream) and the Sabie-Sand River (7.4 km/year downstream) is estimated to be lower than in the Upper Zambezi (53.92 km/year downstream and 27.4 km/year upstream; Nawa et al. 2024) and slightly lower than in the Komati River (8 km/year downstream and 5 km/year upstream; Nunes, Zengeya, Hoffman, et al. 2017). Local hydrology and geomorphology are a driving factor in crayfish invasion progression through a system with strong flows and steeper gradients hindering expansion (Light 2003; Bubb et al. 2004; Mathers et al. 2020). The management of the KNP rivers has been focused on the implementation of Resource Directed Measures to ensure sufficient flow and water quality in the Crocodile and Sabie Rivers (Incomati Basin) and Olifants River (Limpopo Basin) during the dry winter (Pollard et al. 2011; McLoughlin et al. 2021; Riddell et al. 2022). The e-flow regulations in the KNP may be acting as a modifier of crayfish movement, like some sites in the Komati River (Nunes, Zengeya, Hoffman, et al. 2017). Having evolved in billabongs characterised by drying-wetting regimes, redclaw crayfish respond to water current during dying events by moving upstream (Barki et al. 2010). This could explain the high upstream spread rate, in tandem with the annual flood connectivity in the Zambezi (Nawa et al. 2024), as well as the low upstream movement through the perennial reaches of the rivers within the park. Although it cannot be ruled out that the four juvenile redclaw crayfish caught during electrofishing at Nsikazi Confluence have not drifted down from upstream reaches, outside of the park. The Van Graan Dam on the Crocodile River may be a barrier to downstream invasion, although crayfish have been found below the Kariba Dam wall, which is orders of magnitude higher (Douthwaite et al. 2018; Madzivanzira et al. 2021a). Regardless, the stable hydrological characteristics of the dam are facilitating high crayfish abundance and acting as an invasion core and should be the target site for control interventions, especially as it sits on the southernmost border of the park (Barnett and Adams 2021; van Wilgen et al. 2022).

The population is female biased, indicating investment in reproduction, but with no difference across invaded sites or invasion cores, showing that both males and females are pushing the range expansion. Although redclaw crayfish are multiple spawners, no berried or ovigerous females were caught during this sampling (Barki et al. 1997; Reynolds 2002). In addition, there was a low proportion of intersex individuals, which are thought to be expressed more in younger invasions to support rapid colonisation (Levy et al. 2020; Madzivanzira et al. 2021a; Nawa et al. 2024). Albeit low sample size, restricted sampling season and trapping-related biases may be masking long-term population dynamics (Ogle and Kret 2008; Gherardi et al. 2011; Leland et al. 2012; Hudina et al. 2012; Nawa et al. 2024). As expected, the carapace length and mass of the KNP redclaw crayfish population are smaller and lighter than those of the more established invasions in the Upper Zambezi, but like the Komati population and the Barotse Floodplain invasion at a similar time point (Nunes, Zengeya, Hoffman, et al. 2017; Madzivanzira et al. 2021a). Spatial sorting does not appear to be acting on dispersal traits in the Kruger National Park, which may be due to geomorphological differences in the riverine habitats compared to the grassy and ponded Barotse Floodplain, as well as the small sample size (Hudina et al. 2012; Nawa et al. 2024).

There were no signs of ecological impact through competition mechanisms on functionally analogous Potamonautid crabs. Two potential hypotheses were tested for, niche similarity and vacant niche, where niche similarity predicts high impact on similar species (i.e., freshwater crabs) or limited realized impact due to filling a vacant niche and therefore not directly competing with native species (Herbold and Moyle 1986; Lodge et al. 2012; Daly et al. 2023). Our results indicate some support for the vacant niche theory but these conclusions are equivocal for the following reasons. Zengeya et al. (2022) found 60% overlap in resource use between the crab *Potamonautes sidneyi* and redclaw crayfish in the Komati River, showing that the crayfish population is directly competing for trophic resources (i.e., not occupying a vacant niche). The main prey items were gastropods, vegetation, aquatic insects and other crayfish, with a higher trophic position in lotic environments compared to lentic habitats (Zengeya et al. 2022). Redclaw crayfish are flexible omnivores, which, like most crayfish, have the capacity to consume a broad range of resources and are not likely to be resource limited in the KNP (Marufu et al. 2018; Zengeya et al. 2022; Baudry et al. 2024a, 2024b). When lower in body mass, Potamonautid crabs have a lower crushing force than redclaw crayfish, which may affect resource holding potential and outcomes of agonistic contests over shelter, forcing habitat partitioning and thereby reducing trophic competition (Miranda et al. 2016; South et al. 2020). Freshwater crab abundance appears to be low overall, as noted by Zengeya et al. (2022); thus, they have lower per capita consumption, which may make signals of competition hard to detect. This is supported by low relative abundance throughout the Upper Zambezi (Data S3).

Crayfish invasion nor crayfish relative abundance did not affect the structure of fish or macroinvertebrate assemblages. Besides polytrophic omnivory and opportunistic feeding, temporal effects of time since invasion (i.e., cumulative impact) and population abundance (i.e., per capita impact) may be currently keeping the extent of potential ecological impacts at bay. Another globally invasive crayfish, the signal crayfish (*Pacifastacus leniusculus*) causes disruption of macroinvertebrate and fish communities in the United Kingdom, but these effects were only seen after incorporation of long-term monitoring datasets of between 7 and 16 years (Mathers et al. 2016; Galib et al. 2022). Therefore, although redclaw crayfish can certainly exert negative ecological impacts through predation on fish and invertebrates, the actual impact on the aquatic communities of the KNP may be limited by the population currently being in the inflexion stage (Madzivanzira et al. 2021b; Marufu et al. 2018; Zengeya et al. 2022; Soto et al. 2023; Baudry et al. 2024a, 2024b). We recommend adopting a functional trait-based approach to allow better comparison across taxonomically distinct assemblages as well as providing a more informative metric relating to ecosystem function (Mathers et al. 2023). Direct predation by crayfish on adult fish is possible, but this is restricted to small sized benthic fish (Galib et al. 2022). Instead, effects will be seen on eggs, fry and young of the year (Peay et al. 2009; Madzivanzira et al. 2021b). Therefore, adopting aspects of traditional fisheries stock assessment to annual biodiversity monitoring campaigns would be worthwhile to detect long-term changes in length-weight relationships and cohort recruitment patterns caused by redclaw crayfish invasions.

Maintaining the ecological integrity of protected areas is fundamental to their creation and purpose. Biological invasions can threaten all facets of the ecosystem and should be a management priority to curtail (Baard et al. 2017; Moodley et al. 2022; Cuthbert et al. 2022). There are practical limitations and financial limitations to this as crayfish invasions are practically impossible to eradicate once established, especially in large systems; therefore, management ought to focus on restricting spread and reducing localised population abundance through mechanical removal (Hein et al. 2007; Stebbing 2016). Ensuring regular environmental flow regimes, including natural flooding events, may limit crayfish range expansion and dampen ecological impact on macroinvertebrates (Kerby et al. 2005; Kats et al. 2013; Mathers et al. 2020; Satmari et al. 2023). Although flood events are also expected to spread propagules downstream (Madzivanzira et al. 2021a; van Wilgen et al. 2022; Nawa et al. 2024), environmental flow management could be an important nature-based solution, which is cohesive with the KNP overall commitments to environmental flows in the transboundary Inkomati and Limpopo Basins.

5 | Conclusion

The establishment of a new and spreading redclaw crayfish population in the Sabie-Sand River and the range expansion in the Crocodile River are causes for concern and should be monitored more regularly to determine shifts in community and ecosystem function. Beyond community restructuring, specific concerns include the endangered fish *Serranochromis meridianus*, which is present in the Sabie River, including at sites already invaded by crayfish, and although not sampled in this survey, critically endangered *Chiloglanis bifurcus* is a benthic rheophilic species that may be vulnerable to predation by crayfish. There is a paucity of baseline ecological data on Potamonautid crabs, which makes tracking metrics of change difficult. To begin to remedy this, we provide a dataset for freshwater crab morphometrics and relative abundances across water bodies in South Africa, Namibia, Zambia and Zimbabwe as a starting point for long-term monitoring of both crayfish and crabs (Data S3).

African freshwaters are undervalued and understudied, leaving the systems and the people that rely on them at risk from unabated ecological degradation. This will be the third call to action for practical solutions regarding crayfish in the KNP, which echoes sentiments from the Upper Zambezi catchment. The KNP and the private reserves making up the Greater KNP contribute US$ 370 million a year to the South African economy (Chidakel et al. 2020). The social and financial resilience of this economy relies on tourists who come to observe unique, undegraded wilderness areas and the species found within. Water resources underpin the functioning of both the ecosystem and the facilities provided by the park and concessions. Management of the redclaw crayfish invasion needs to be cohesive both inside and outside of the national park; therefore, considerable investment and institutional collaboration are essential to afford freshwater environment protection in the same way as terrestrial landscapes.

Author Contributions

Conceptualisation: Josie South and Dumisani Khosa. Project administration: Josie South and Dumisani Khosa. Methodology: Josie South, Dumisani Khosa, Angelica Kaiser-Reichel, Esi Bossman and Mmathapelo Mthembu. Formal analysis: Josie South and Olivia Stubbington. Visualisation: Josie South, Olivia Stubbington and Taylor Maavara. Writing – original draft: Josie South. Writing – review and editing: Josie South, Olivia Stubbington, Angelica Kaiser-Reichel, Esi Bossman, Nikisha Singh, Mmathapelo Mthembu, Taylor Maavara, Gordon O'Brien, Kedibone Masenya and Dumisani Khosa. Funding: Josie South, Dumisani Khosa, Gordon O'Brien and Taylor Maavara.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare (at https://figshare.com/account/articles/29254412).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.