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Research paper

Exploring spatial transferability of expert-derived river ecosystem indicators and driver-response relationships in southern Africa

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Interactive, ecosystem-based environmental flow models provide stakeholders with a wide range of useful information, such as scenario analysis of trade-offs between social and ecological impacts and river infrastructure expansion for various development pathways. However, their adoption remains restricted in data-limited environments partly because of the difficulty in developing the driver-response relationships that form the heart of ecosystem-based models. Such relationships describe ecological responses to environmental drivers and are perceived to have limited transferability from previously studied river basins. To test this perception, this study extracted and synthesized expert-derived ecosystem indicators and driver-response relationships developed for 63 sites across 20 rivers in southern Africa and evaluated the factors that determined transferability of indicators and relationships between river sites. The assessment revealed that, in general, ecosystem indicators and responses were not dictated by river type (in terms of longitudinal zone, broad habitat type, and valley slope) as calculated by continental scale datasets available for southern Africa. Instead meso-habitats played a key role in determining the ecosystem indicators and links between them. Riparian vegetation and macroinvertebrate indicator guilds had functionally similar links even as the species and underlying river type varied between sites. Expert-derived driver-response relationships were found to be convergent across a range of specialist teams and project time allocations. These findings support the spatial transferability of driver-response relationships for scenario analysis across southern Africa. Further, they provide the foundation for the development of generic ecosystem indicators and driver-response relationships for geomorphology, riparian vegetation, macroinvertebrate and fish indicators that can be used for rapid environmental flow assessments of rivers to support informed decision making related to river infrastructure development.

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INTRODUCTION

'Environmental flows' (EFlows) describe the quantity, quality and pattern of the flows of water, sediment and biota required to support different levels of ecological functioning in riverine ecosystems, and the human livelihoods and well-being that depend on these ecosystems (amended from the Brisbane Declaration, 2007). Over time, methods for the assessment of EFlows have evolved from simple hydrological ratios used to set minimum flows (e.g., Tennant, 1976) to ecosystem-based models that simulate links between key components of aquatic ecosystems through driver-response relationships (Poff et al., 2017). The latter are also referred to as flow-ecology or stressor-response relationships (Horne et al., 2019; Hughes and Louw, 2010; Hughes et al., 2014; O'Keeffe et al., 2002; Rosenfeld et al., 2022). EFlows assessment methods that use driver-response relationships include models and methodologies such as 'downstream response to imposed flow transformations' (DRIFT; Brown et al., 2013), 'ecological limits of hydrologic alteration' (ELOHA; Poff et al., 2010), 'ecosystem functions model' (HEC-EFM; Hickey et al. 2015), and 'physical habitat simulation software' (PHABSIM; Stalnaker et al., 1994).

Driver-response relationships are a recommended basis for contemporary EFlows assessments (King and Brown, 2010; Poff et al., 2017; Praskievicz and Luo, 2020), but their adoption remains limited because of the expertise and time required to develop the relationships (Davies et al., 2013; Salinas-Rodríguez et al., 2021) and their perceived limited transferability between river sites (Poff and Zimmerman, 2010; Olden and Liermann, 2009). If such relationships can be shown to be spatially transferrable, then those developed for one river can be used for other rivers, thereby offering the possibility of in-depth river modelling at relatively low cost (Chen, 2017). Existing evaluations of the transferability of driver-response relationships are from data-rich rivers in Europe and North America. Chen and Olden (2017) evaluated the transferability of flow-ecology relationships for fish species across the southwestern United States and found that they could be transferred across space and time, although transferability was higher among free-flowing rivers than regulated rivers. Bower et al. (2022) explored how flow-ecology relationships for fish and macroinvertebrates varied across rivers in South Carolina and found that, although the direction of response was the same, the shape and magnitude of some relationships varied across freshwater ecoregion and hydrological river class. Similarly, Praskievicz and Luo (2020) analysed flow-ecology relationships across the southeastern United States and found that high-flow duration and frequency, along with 3-day maximum and minimum flows, were consistently important in impacting ecological metrics.

There are few formal assessments of the transferability of such relationships in data-poor environments, despite a growing demand for EFlows assessments to guide sustainable hydropower development in the developing world (King and Brown, 2021; Tonkin et al., 2014). Therefore, the objective of this study was to determine whether driver-response relationships were consistent and transferrable across rivers in southern Africa and, if so, provide guidelines to develop generic ecosystem indicators and associated driver-response relationships for this region to promote the use of such relationships in EFlows and other river assessments such as environmental impact assessments and cumulative impact assessments. Once established, such models can inform estimates of the likely response of freshwater ecosystems to planned water-resource management and development (e.g., Beilfuss and Brown, 2010; King et al., 2014) through an enhanced understanding of river functioning in the region. This knowledge base supports the objectives of Sustainable Development Goals 6.5 and 6.6, which advocate integrated water resource management and the protection of water-related ecosystems (Brown et al., 2020).

The assessment focused on indicators and driver-response relationships compiled by different teams of regional specialists and used in DRIFT databases of southern African rivers. It was expected that river type, defined in part through slope, freshwater ecoregion, valley setting and climatic zone, would be factors in the choice of indicators and driver-response relationships, but that other factors could also play a role (Dallaire et al., 2019). Such factors include baseline ecological state (e.g., Kleynhans, 1996), budgetary constraints in the development of each database, and possible bias arising from the use of expert opinion (Krueger et al., 2012; de Little et al., 2018; Webb et al., 2015). The latter was relevant, since if the DRIFT databases contained divergent driver-response relationships based on the composition of the compilation team, this would call into question the use of these expert-derived driver-response relationships in guiding decision making in the region. Therefore, particular attention was paid to the level of consistency, in relation to expert opinion, within and across existing DRIFT databases included in the sample set.

Overview of the DRIFT method

DRIFT is an ecosystem-based model developed in South Africa (King et al., 2004), and is used extensively in Africa and Asia to predict the impacts of water-resource developments on rivers, wetlands, lakes, and estuaries (e.g., Seaman et al., 2016; Brown et al., 2019; Brown et al., 2022). It is increasingly used in river restoration, cumulative impact assessments and basin management and planning (e.g., Brown et al., 2013; King et al., 2014; Hughes, 2015).

In DRIFT, the aquatic ecosystem is represented by a suite of disciplines that typically include hydrology, hydraulics and/or hydrodynamics, sediment supply, water quality, geomorphology, riparian vegetation, macroinvertebrates, fish and wildlife, and social uses. Hydrology, hydraulics, hydrodynamics and sediment supply (measured or modelled) are generated outside of DRIFT and imported as time-series data, usually at a daily time-step (Joubert et al., 2022). DRIFT divides the input time series into seasons and calculates several ecologically relevant indicators for each, such as the duration, the time of onset, and 5-day minimum and maximum flows of water. The remaining disciplines are populated by specialists who select indicators to represent the ecosystem, define links between the indicators and construct driver-response relationships using their experience and knowledge (Martin et al., 2012), combined with field sampling and surveys, local wisdom, available data, and the scientific literature (Joubert et al., 2022). The flexibility to use multiple information sources has supported the adoption of DRIFT in data-poor environments (Overton et al., 2014). The x-axes of DRIFT driver-response relationships have 7 points which include the median, minimum and maximum value of the driver that occurs in the baseline time series (Fig. 1). These data points are used to capture the response based on the knowledge of the states of the responding indicator (Wheeler et al., 2018). Each DRIFT database houses hundreds of driver-response relationships that simulate the key links in the aquatic ecosystem under study. Specialists also document the reasoning, supporting data, and literature underpinning each relationship.

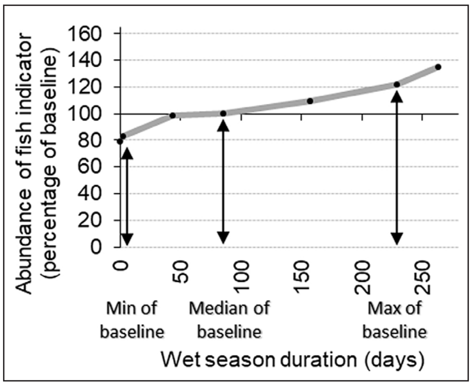


Figure 1. An example of a driver-response relationship linking floodplain fish to the duration of the wet season from the Cubango-Okavango DRIFT database (King et al., 2014)

METHODS

Ten DRIFT databases, representing 63 sites on 20 southern African rivers, were obtained from Southern Waters Ecological Research and Consulting cc (Table 1; Fig. 2). The procedures used to set up a DRIFT model include numerous cross-checks for correctness and consistency, several layers of internal review and often rigorous external review (e.g., by national regulatory bodies and international organizations that use model results). Three of the ten selected databases were published in peer-reviewed scientific literature, viz., for the Cubango-Okavango Basin (King et al., 2014), Pongola Floodplain (Birkhead et al., 2018; Brown et al., 2018), and the Elephant Marsh on the Shire River (Birkhead et al., 2022a; Birkhead et al., 2022b; Brown et al., 2022). The analyses focused on indicators and relationships under 4 ecosystem disciplines: geomorphology, riparian vegetation, macroinvertebrates and fish, as these are basic components of the river ecosystem and important for evaluating river health (Kennard, 2005; Maddock, 1999; Riis et al., 2020).

Transferability across river type

The sites were categorized by longitudinal geomorphic zone (Rowntree et al., 2000) based on river gradient (Linke et al., 2019), major habitat types (MHT) from the Freshwater Ecoregions of the World (Abell et al., 2008) and site valley profile based on terrain slope (Linke et al., 2019) defined as 'flats' with zero terrain slope, 'river' with terrain slope of 1° to 50°, and 'gorge' with terrain slope > 50°. The indicators and driver-response relationships used at each site were compared (including the selection of indicators, and the shape and magnitude of the relationships) within and between river types.

Transferability across varying hydrology

Each site has a different hydrological regime based on climate and catchment characteristics and the period of record. Consequently, the x-axes of hydrological relationships varied across sites. Generally, for driver-response relationships at a single site, the size of the response correlates with how far the driving indicator is from its median baseline value (e.g., Fig. 1). To assess whether

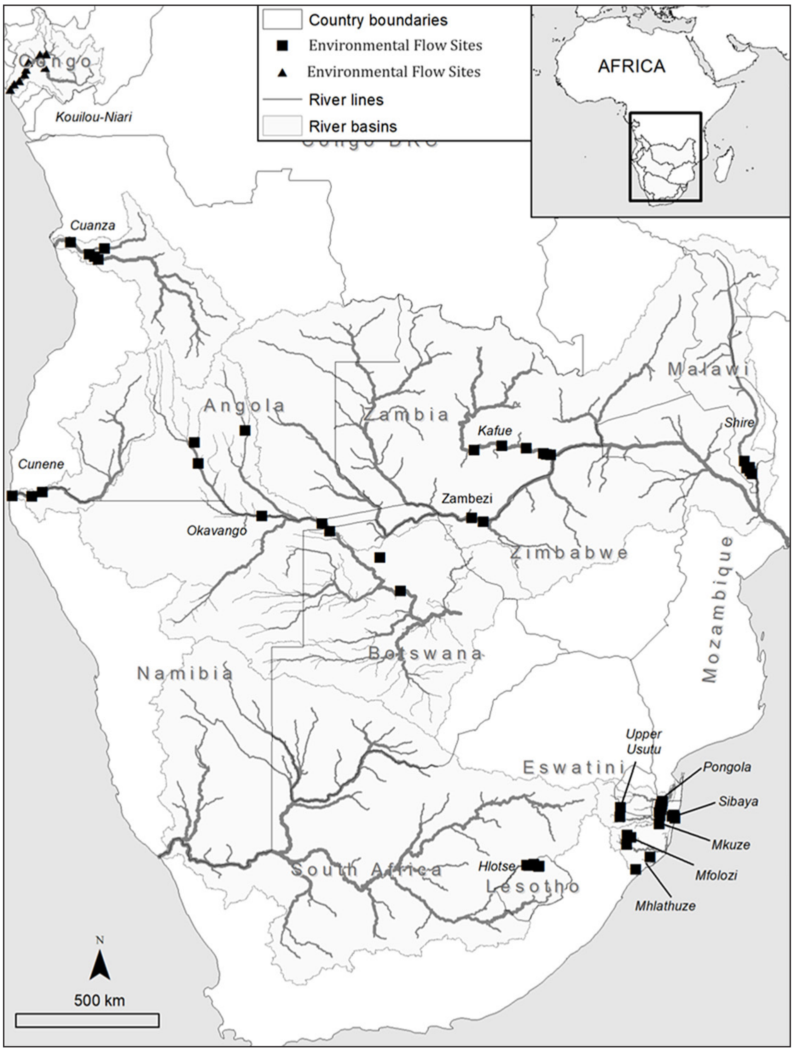


Figure 2. The locations of the 63 sites included in the DRIFT databases

Table 1. Key information on the 10 DRIFT databases included in the assessment

No.	Project/study	River and no. of sites	Country	~Study date
EFlows assessment studies for infrastructure such as hydropower projects (HPPs)				
1	EFlows assessment for Batoka Gorge HPP (Southern Waters, 2019)	Zambezi (2)	Zimbabwe, Zambia	2019
2	EFlows assessment for Baynes HPP (Southern Waters, 2022)	Cunene (3)	Angola, Namibia	2022
3	EFlows assessment and water quality modelling for Lesotho Lowlands Water Development Project (Multiconsult et al., 2022)	Hlotse (5)	Lesotho	2022
4	EFlows assessment for Sounda HPP (Hughes et al., 2017)	Kouilou (8), Niari (1)[1]	Republic of Congo	2017
5	Cumulative impact assessment for hydropower development (Hughes, 2015)	Cuanza (4), Lucala (1)	Angola	2015
Basin planning studies				
6	Climate resilient livelihoods and sustainable natural resources management in the Elephant Marsh, Malawi (Brown et al., 2022)	Shire (5)	Zambia	2016
7	Comprehensive EFlows Assessment of the Lower Kafue Sub-catchment (Brown et al., 2021)	Kafue (6)	Zambia	2021
8	Cubango-Okavango Basin and Programme for Transboundary water management in the Cubango-Okavango River basin (King et al., 2014)	Cubango (1), Cwebe (1), Cuito (1), Okavango (4), Boteti (1)	Angola, Botswana, Namibia	2014
Reserve determination studies				
9	Reserve determination in the Usutu-Mhlathuze Water Management Area (WMA) (DWS, 2015)	Mhlathuze (2), Mfolozi (3), Mkuze (1), Upper Pongola (1), Upper Usutu (1)	South Africa	2015
10	Reserve determination in the Usutu-Mhlathuze WMA (Brown et al., 2018)	Pongola (12)	South Africa	2018

[1] The Kouilou and Nairi rivers are not in southern Africa but included in the assessment because they share many characteristics with west coast rivers in Angola where the hills rise sharply from the coastal lowlands and form a high escarpment (Huntley, 2019; Dallaire et al., 2019).

this applied across sites – i.e., did river sites with large natural variation have commensurately larger responses to hydrological change as compared to those with lower baseline variation – it was tested whether the natural variability of the river hydrology at the site was correlated with the size of the response. A high correlation would indicate that when transferring a relationship from a river site with low natural variability in hydrology to one with high natural variability, the size of the response should be increased, and vice versa. To test this, the correlation between the baseline extreme values of the hydrological drivers (the minimum and maximum value as a percentage of the median value) and the corresponding percentage change in the responding ecosystem indicators (as estimated by the driver-response relationships) was calculated. These analyses were performed at the discipline level using the full dataset of all sites.

Influence of other factors

Sites were grouped based on other factors that could influence driver-response relationships, and the sensitivities of driver-response relationships were compared between groups. The ecological state for each discipline at each site was ranked by the specialist teams from an 'A' (pristine natural condition) to 'F' (seriously modified condition; Kleynhans, 1996) when the driver-response relationships were developed. Based on these rankings, sites were classified as natural ('B' or higher) or modified with respect to each discipline. In an ideal world, such databases would be founded on empirical or long-term measurements, but these do not exist for the basins for which DRIFT was set up, and so the relationships were developed with available resources, with time and budget constraints influencing scope. Project time allocation (categorised as 'low' or 'medium'; 33 and 30 sites, respectively) was used as a proxy of the effective project budget as it quantifies the time and effort expended on activities such as field visits, literature searches and construction of response relationships and external modelling for each project. Lastly, some sites had flashy hydrology (characterised by multiple flood events spread across the year) and others had flood-pulse hydrology (with a single well-defined flood season; Junk et al., 1989). The sensitivities of the driver-response relationships were calculated at the discipline level for each site (Equation 1) and compared between the groups described. Only default DRIFT hydrological drivers (Joubert et al., 2022) were used as these were common across all sites (e.g., duration and onset of seasons and average seasonal flows).

$$\text{Average site sensitivity to change} = \frac{1}{m}\sum_{j=1}^{m}\frac{1}{n}\sum_{i=1}^{n}|Z_{i,j}|+|Y_{i,j}| \quad (1)$$

where:

m = number of discipline indicators at the site

n = number of hydrology driver-response relationships for each indicator

$Z_{i,j}$ = % change in indicator j against baseline maximum value of driver i as quantified by relevant driver-response relationship

$Y_{i,j}$ = % change in indicator j against baseline minimum value of driver i as quantified by relevant driver-response relationship

RESULTS

Overall, the dataset comprised over 7 000 driver-response relationships. However, as there was no overarching guiding framework, these differed subtly from each other. This meant that there were many ecosystem indicators and qualitatively different links that could not be compared directly. In total, there were 70 geomorphology indicators with 309 unique driver-response relationships; 52 riparian vegetation indicators with 328 relationships; 46 macroinvertebrate indicators with 275 relationships and 76 fish indicators with 569 driver-response relationships.

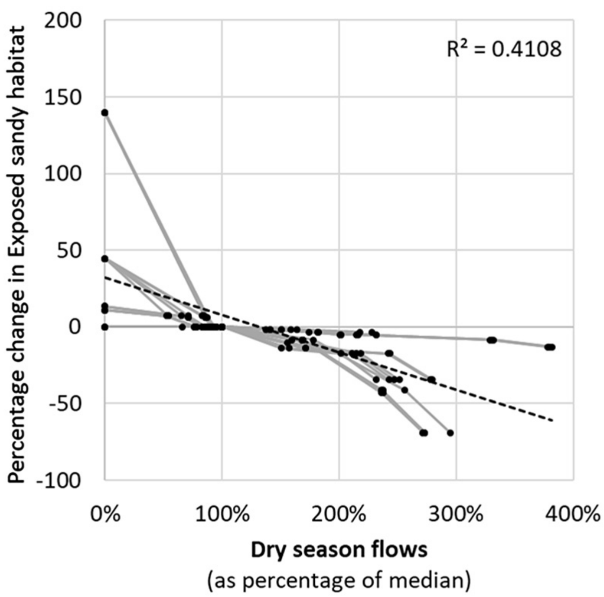
Transferability across river type

Geomorphology

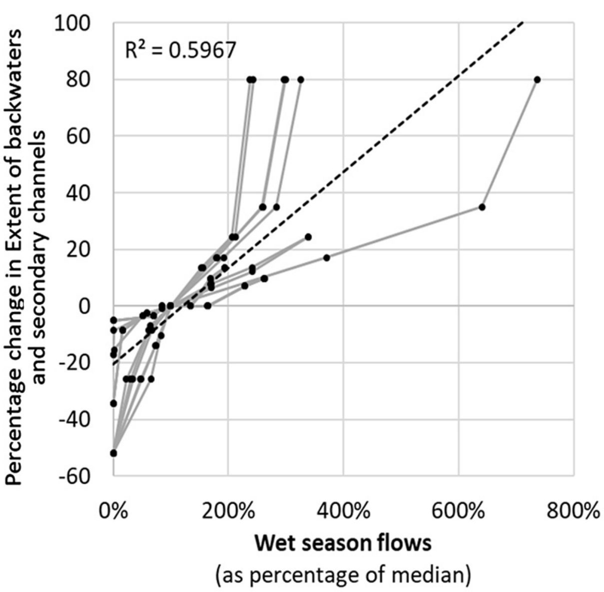
After streamlining the datasets based on indicator names and descriptions (e.g., 'bed coarsening/fining', 'bed material grain size', 'bed sediment conditions', and 'channel bed sediment' were combined into 'bed sediment size'), 20 geomorphology indicators remained. Subsequently, 2 sub-groups of geomorphology indicators emerged. The first was those broadly applicable to all rivers and river types, such as bed sediment size, bed erosion, bank erosion, and turbidity. Of these, bed sediment size was the most used. It was included in 75% of sites and was used across tropical and subtropical sites, all slope classes and all except two MHT. The second subgroup of indicators were specific to meso-habitats present at a site. Of these, some occurred frequently (at about a third of the sites), e.g., 'extent of exposed sandy habitat', 'backwaters and secondary channels', and 'vegetated islands'. Others such as 'rapids', 'lakes', and 'anastomosing reaches' were only used at a handful of sites. In both cases inclusion was not dependent on river type as defined by longitudinal zone, MHT, and valley slope; these indicators were used across many river types and instead depended on the habitats recorded at each site.

Sites located on rivers with floodplains had a set of floodplain-specific indicators (e.g., 'extent of inundated floodplain' and 'floodplain sediment deposition'). The continental-scale datasets used for river typing only identified large floodplains such as the Elephant Marsh or the Okavango Delta and did not distinguish between river sites with and without smaller riparian floodplains (and so did not assist with predicting the use of floodplain indicators). For sites with large floodplains, such as the Okavango Delta, external hydraulic and hydrodynamic models were used to calculate the response of the floodplain geomorphology, which obviated the need for expert-derived floodplain geomorphic indicators.

The drivers of change in the geomorphology indicators were related to the level of inundation and erosion potential, which were consistent across sites (e.g., Fig. 3). Notwithstanding the consistency in the responses for geomorphology indicators, the definition of the indicators varied between study teams. For instance, pool depth was defined as the geomorphic depth of pools by some specialists and the depth of the water within pools by others; the area of sand bars referred to the total area of sandy habitat or only to the extent exposed in the dry season; and cut banks quantified the total extent of cut banks, which may increase due to bank slumping driven by flow changes or the extent of natural cut banks that contain important habitat. Further, different specialists quantified the level of inundation through links to different hydrological indicators (e.g. maximum 5-day wet season flow, total flood volume, or average flows in the wet season were used to represent flood flows). Some specialists also used intermediate indicators, whereas others did not. For example, at 15 sites hydrology and sediment supply was linked to an 'erosion' indicator, which was then linked to bed sediment size, and at the remaining sites erosion was not used as an indicator and instead hydrology and sediment supply were linked directly to bed sediment size. These factors meant that the relationships were not directly comparable across many sites, although the underlying rationales and explanations were consistent. Furthermore, sediment indicators were handled differently by specialist teams, and these could not be reconciled as they did not fully overlap. For example, certain databases used 2 sediment indicators: suspended load and bedload; whereas others used clay and silt; sand and gravel; and cobbles and boulders. Although, cobbles and boulders typically travel as bedload, coarse sand may travel as either bedload or suspended load and, depending on the mode of transport, interacts differently with the environment; for example,

<table>
<tr><th>Driver-response relationship</th><th>Notes</th></tr>
<tr><td>
</td><td>Data source: 23 sites from 5 databases
Rivers: Zambezi, Kafue, Cuanza, Lucala, Cunene, Cubango, Cwebe, Cuito, Okavango, Kouilou

Longitudinal zones: low land, lower foothill, upper foothill
Valley slopes: flats, gorge, river

Major habitat types: tropical & subtropical upland rivers; tropical & subtropical floodplain rivers & wetlands; tropical and subtropical coastal rivers; xeric freshwaters & endorheic basins</td></tr>
<tr><td>
</td><td>Data source: 14 sites from 4 databases
Rivers: Zambezi, Cunene, Okavango, Kouilou

Longitudinal zones: low land, lower foothill, upper foothill
Valley slopes: flats, gorge, river

Major habitat types: tropical & subtropical floodplain rivers & wetlands; tropical and subtropical coastal rivers; xeric freshwaters & endorheic basins</td></tr>
</table>

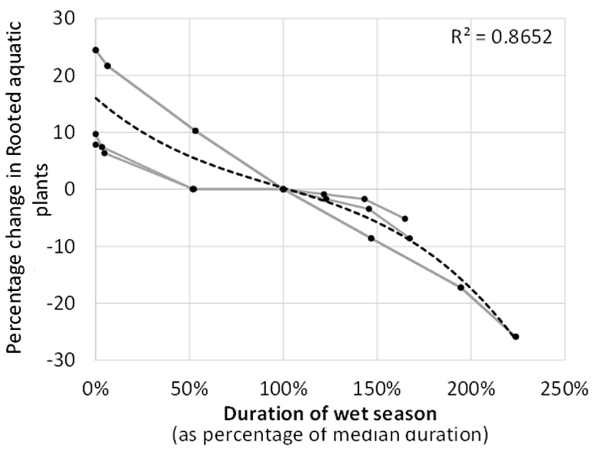
Figure 3. Illustrative examples of geomorphology driver-response relationships showing consistency across sites

the mode of transport of sand determines the proportion that would be trapped behind a dam. The level of sediment suspension of the different size fractions is influenced to a degree by the slope or longitudinal geomorphic zone of the river.

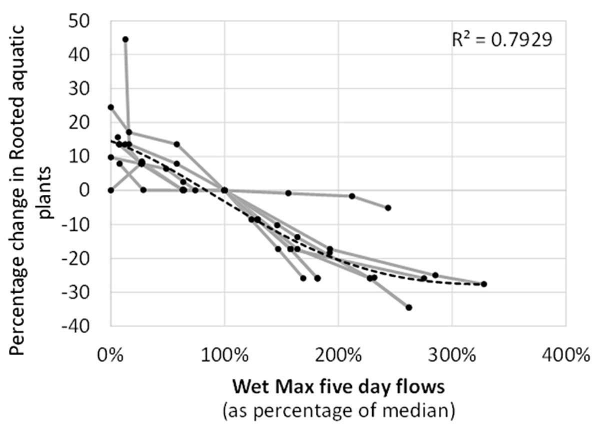
Riparian vegetation

Riparian vegetation is typically distributed laterally up a riverbank in a sequence of vegetation zones, e.g., aquatic, emergent, wet bank, transitional and dry bank (Reinecke et al., 2015; Reinecke et al., 2022). In the databases studied, riparian vegetation indicators were not explicitly aligned to these zones. After grouping indicators by lateral zone based on the supporting explanations (e.g., indicators named 'emergent macrophytes', 'marsh emergents', 'lower wet bank', and 'papyrus' were grouped under the 'emergent zone'), the driver-response relationships across sites were similar (Fig. 4). The most frequently used indicators were those that represented wet bank and dry bank zones (75% of the sites), followed by those for transitional (43%), aquatic (35%) and emergent (16%) zones. There was also a specific set of indicators used at sites with floodplains (e.g., floodplain grasses). Sites on upper foothill river sites did not include any floating aquatic indicators, and floodplain vegetation indicators were not used at sites in gorges. Other than these limited observations, insufficient evidence was found to link the indicator selection or the shape of the response to river type.

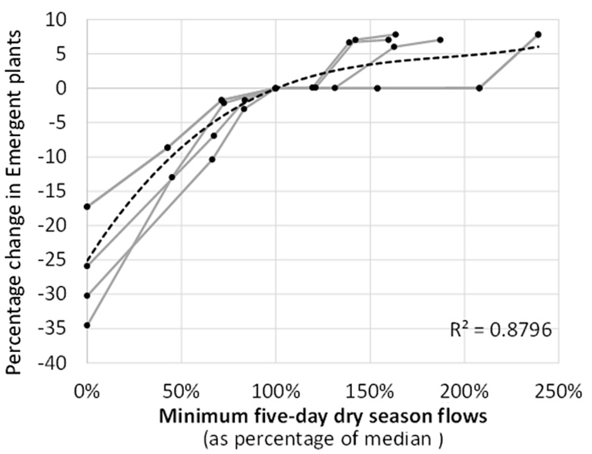
Although the species present in each zone varied across sites, the functional behaviour, and responses to drivers within lateral vegetation zones, were consistent. While this was broadly applicable, in certain cases, driver-response relationships were species-specific (Fig. 5). For instance, *Phragmites mauritianus* are evergreen reeds that grow and proliferate in the dry season in response to elevated dry season flows, whereas *Phragmites australis* are dormant in the dry season and are drowned by elevated flows in the dry season (Van Coller et al., 1997, Kettenring and Whigham, 2009). Similarly, acacias have shallow roots and so can destabilize riverbanks whereas *Salix babylonica* (English Willow) and *Populus canescens* (Grey Poplars) have deep roots and stabilize banks (Reinecke et al., 2015; Rowntree, 1991). The presence of different species was not found to be dependent on river type. For instance, *Acacia* spp. and *Salix babylonica* are exotic to Africa, and their presence is dependent on the site and invasion history.

<table>
<tr><th>Driver-response relationship</th><th>Notes</th></tr>
<tr><td>
</td><td>Data source: 5 sites from 3 databases
Rivers: Zambezi, Cunene, Okavango

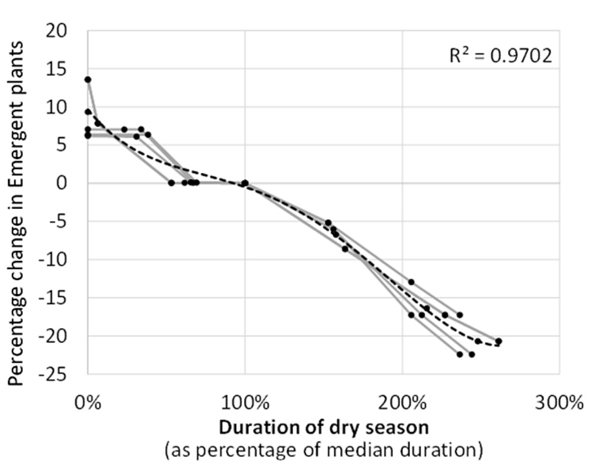
Longitudinal zones: lowland, lower foothill, upper foothill
Valley slopes: flats, gorge, river

Major habitat types: tropical & subtropical floodplain rivers & wetlands, xeric freshwaters & endorheic basins.</td></tr>
<tr><td>
</td><td>Data source: 10 sites from 4 databases
Rivers: Zambezi, Cunene, Okavango, Kouilou, Niari

Longitudinal zone: low land, lower foothill, upper foothill
Valley slope: flats, gorge, river

Major habitat types: tropical & subtropical floodplain rivers & wetlands; tropical and subtropical coastal rivers; xeric freshwaters & endorheic basins</td></tr>
<tr><td>
</td><td>Data source: 5 sites from 2 databases
Rivers: Zambezi, Okavango

Longitudinal zones: low land, upper foothill
valley slopes: flats, gorge, river

Major habitat types: tropical & subtropical floodplain rivers & wetlands</td></tr>
<tr><td>
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Rivers: Zambezi, Okavango

Longitudinal zones: low land, upper foothill
valley slopes: flats, gorge, river

Major habitat types: tropical & subtropical floodplain rivers & wetlands</td></tr>
</table>

Figure 4. Illustrative examples of riparian vegetation driver-response relationships showing consistency across sites. R^2 for polynomial best-fit line.

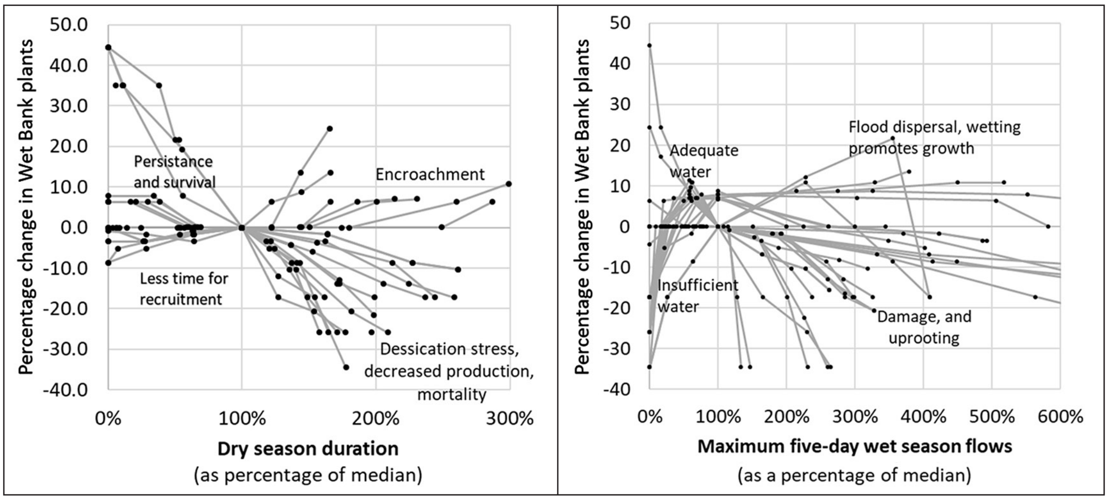

Figure 5. Hydrological driver-response relationships for river wet bank vegetation indicators were not consistent when only considering the lateral zone

Macroinvertebrates

Macroinvertebrate indicators included those based on feeding guilds (e.g., scrapers, filter feeders), order (e.g. Ephemeroptera) and family (e.g., Baetidae, Gomphidae). Indicators defined by family had the most consistent responses across varying river types and study teams. Species-level information was rarely used to define macroinvertebrate indicators. The selection of indicators at a site was defined by the local meso-habitats (e.g., sandy channel beds or bedrock) which were not captured by river type. The linked indicators selected were mostly related to bed sediment size, flow patterns, physical habitat such as backwaters and pools, and the nature and distribution of the riparian and instream vegetation. Thus, as was the case for geomorphology and riparian vegetation, local meso-habitats were good predictors of macroinvertebrate indicators and responses.

Fish

No obvious trends or groups emerged from the 83 fish indicators used across the 10 databases, mostly because of the different approaches adopted by the various fish specialists. Five databases used fish guilds as indicators, but there was limited overlap among the guilds used, e.g., resident habitats ('resident in river', 'rocky specialists', 'sandbank dwellers'), reproductive habitats (e.g., 'guarders–sand nests', 'guarders–bubble nests'), migration patterns (e.g., 'floodplain migrants'); diet (e.g., 'insectivores', 'algivores'), and flood patterns (e.g. 'flood-dependent–benthic', 'flood-independent–generalists'). The remaining 5 databases used individual species as representative indicators of implied (or sometimes explicit) groups or guilds. There were some commonalities as a few species recurred across databases. For example. *Amphilius uranoscopus* was used as an indicator in 3 databases as: small rheophilic species, rock dweller, and as an indicator species. These instances of overlap were, however, limited. Of the 210 species described in the various project reports, only 27 were mentioned in 2 or more databases and only 8 used in greater than 4 databases. With this limited overlap, the methodology adopted in this study was not suitable to describe similarities in indicator selection.

Transferability across varying hydrology

There was negligible correlation between the degree of variation in the hydrology driver from its median value and the response of the ecosystem indicators assessed at the discipline level (Fig. 6): geomorphology (correlation coefficient [ρ] = 0.16; n = 846); riparian vegetation (ρ = 0.15, n = 779); macroinvertebrates (ρ = 0.13; n = 456), and fish (ρ = 0.20; n = 1 071). However, when the distance of the hydrology driver was very close to the median value, i.e., rivers with low natural variability, in most cases the response of the ecosystem indicator was also small (i.e., no responses in the area marked by the grey X in Fig. 6). Subsequently, the analysis was repeated piecewise considering only those data points where the driving hydrology indicator was within 50% value of the median, and found that the correlation increased, low for geomorphology (ρ = 0.43; n = 243) and riparian vegetation (ρ = 0.46; n = 241), and moderate for fish (ρ = 0.53; n = 289). This indicates that transferring relationships from rivers with very high variability to those with very low variability or vice versa may require scaling to the severity of the response, with the severity of the response being constrained by the $x = y$ line in Fig. 6.

Influence of other factors

Baseline ecological state (natural or modified) did not influence the sensitivity of the geomorphological (Wilcoxon test W = 177, n = 41, p > 0.5) or riparian vegetation (Wilcoxon test W = 244, n = 49, p > 0.2) indicators. The sensitivities of the macroinvertebrate and fish indicators were however dependent on their ecological status at the time of study. For macroinvertebrates, the median sensitivity for natural sites was double that of modified sites (Wilcoxon test W = 117, n = 33, p < 0.1, Fig. 7). Conversely, fish were more sensitive at modified sites than natural sites (Wilcoxon test W = 150, n = 56 sites, p < 0.01).

There was no significant difference in the sensitivity of responses between sites from projects with low and medium time allocations for geomorphology, riparian vegetation, and fish disciplines. For macroinvertebrates the median sensitivity was 25% lower for river sites set up with medium time allocations relative to those with low time allocations (Wilcoxon test W = 174, n = 33 sites, p < 0.05). Projects with low time allocations had less dispersion in sensitivity as compared to studies with medium time allocations.

The sensitivities of driver-response relationships with default DRIFT hydrology indicators for geomorphology and fish indicators were lower at sites with flashy hydrology relative to those with flood pulse hydrology (Wilcoxon test p < 0.01; Fig. 7). This was compensated for at sites with flashy hydrology by additional links to the frequency of individual flood events. Flood frequency hydrology drivers used counts of flood events for floods of 8 different sizes up to 1:20 year floods. Although there were no significant differences between sites with flashy and flood pulse hydrology for riparian vegetation and invertebrate indicators, the spread followed a similar trend to the geomorphology and fish.

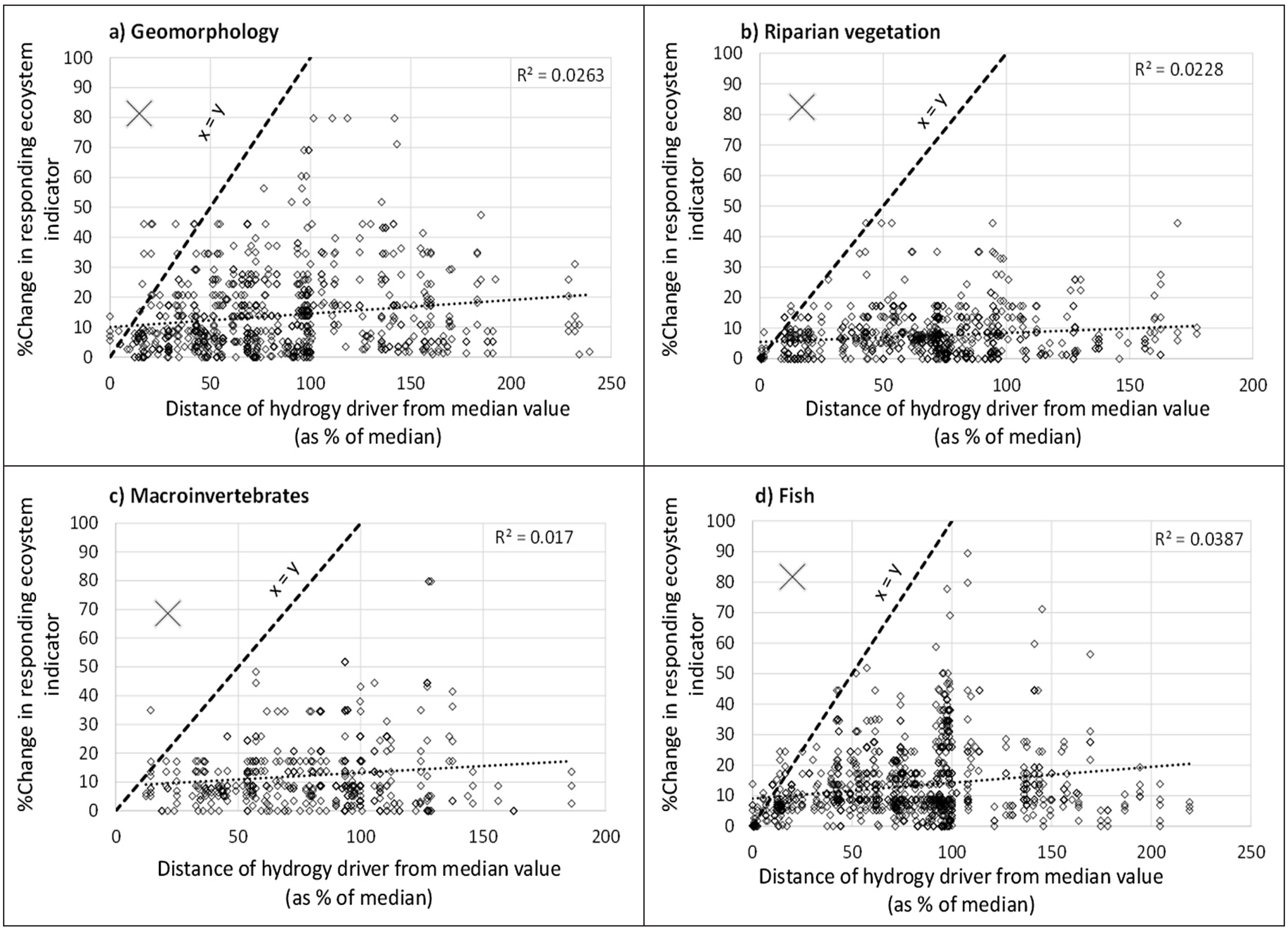

Figure 6. Low correlation between the distance of the driving hydrology indicators from the median (as a percentage of the median) and the response of ecosystem indicators. R^2 provided for linear fit.

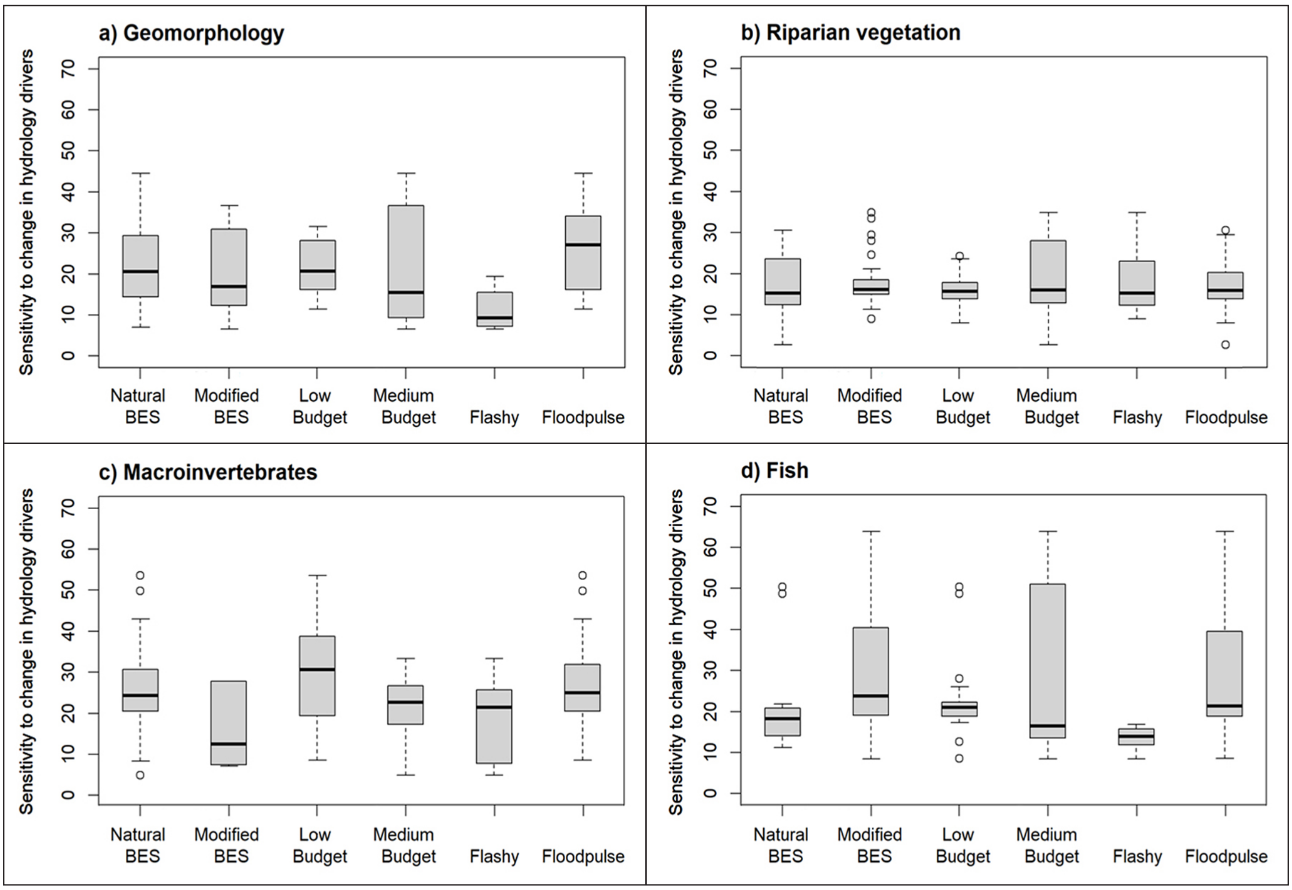

Figure 7. Influence of baseline ecological state, time allocations, and type of hydrological regime on the sensitivty of the 4 disciplines assessed

DISCUSSION

The analyses presented in this study align with the recommendations of Krueger et al. (2012), who suggested that modelling using expert opinion should be used as a learning process, and that relationships so developed, including mistakes made, should be available for peer review to support this learning. Generally, except for fish, selection of indicators, links, and direction of driver-response relationships were found to be transferrable across sites in southern Africa across similar meso-habitats, which affirms the expectations of Stevenson and Sabater (2010), who anticipated that basic ecological principles should be transferrable across different river ecosystems.

Based on available spatial datasets for southern Africa, standard classifications of river type (e.g., Melles et al., 2012; Dallaire et al., 2019) did not affect the indicators or driver-response relationships selected to represent river ecosystem components. Similar indicators and convergent driver-response relationships were used across most river types. Instead, the selection of indicators was strongly influenced by meso-habitats at each site, which can vary in frequency of occurrence across different river types. This was unexpected given the emphasis in the literature on the value of river types in the understanding of aquatic ecosystems, and that meso-habitats are not used in many river classifications (Melles et al., 2014). Higgins et al. (2005) include 'macro-habitats' (1–10 km valley segments) in their freshwater classification but allowed for its omission where fine spatial data were unavailable. Dallaire et al. (2019) mention the importance of 'micro-habitat', but do not include it in their classification, probably because they focussed on factors for which global data are available. The results from this study are, however, supported by Cubley et al. (2022), who found that localised hillslope and valley setting were drivers of the transferability of riparian vegetation guild data across rivers in the Colorado Basin; although, like Dallaire et al. (2019), available continental-scale spatial data for valley setting and hillslope were too coarse to distinguish these differences. This may change with recent advances in remote sensing and computational analysis techniques that are increasingly able to identify reach-scale features, including meso-habitats and other finer resolution details such as grain size distributions (Piégay et al., 2020). While the theory around such techniques is developing rapidly, availability of data outputs from such processes remains limited in southern Africa and is a potential area for future work.

Despite relatively consistent driver-response relationships across river type, specialist teams and time allocations, many driver-response relationships were not directly comparable between databases. There were 3 main reasons for this: (i) specialists selected slightly different summary statistics as drivers for the same indicator with no reasons provided for picking one over another; (ii) the definitions of ecosystem indicators differed across databases even though the intent was to model the same component of the ecosystem; and (iii) some specialists used direct links to flow and sediment indicators whereas others used intermediary indicators. The different approaches, while inconsequential in the context of individual studies, resulted in difficulty in quantitative comparison between databases, which reduced the usefulness of information on ecosystem functioning generated (Martin et al., 2012). To address this shortcoming, and using the findings presented in this study, Bukhari et al. (2024) proposed a list of 57 pre-defined ecosystem indicators covering geomorphology, riparian vegetation, macroinvertebrate and fish, with a combined 205 driver-response relationships. For rapid EFlows assessments, indicators may be selected from this library based on the meso-habitat present at the study river site. For fish, indicator guilds are suggested to be defined based on primary resident habitat, which can then be supplemented with driver-response relationships specific to diet, migration, and reproductive behaviour (e.g., Welcomme et al., 2006) that may be selected based on available information on the fish present at the river site under study. The framework provides a uniform baseline for future studies to support the generation of directly transferable data for southern African rivers.

The status of macroinvertebrates and fish are assessed using health indexes such as the South African Scoring System (SASS; Dickens and Graham 2002) and Fish Assemblage Integrity Index (FAII; Kleynhans 1999), which classify the ecological status based primarily on diversity, with modified sites consisting of more tolerant taxa as compared to those present at natural sites (Laasonen et al., 1998) and subsequently less sensitive to changes in hydrology. However, with fish, additional factors such as adult size and abundance, as assessed through field surveys and interviews with fishermen, are also used when assessing the health status of the fish. Possibly due to this, it is conceivable that fish are assessed to be in a modified state due to lowering of abundance and smaller adult sizes, before a move towards more tolerant taxa has occurred, and therefore modified sites were assessed to be more vulnerable to hydrological change (Planque et al., 2010).

Reassuringly, the amount of time allocated to specialists did not influence the average sensitivity of driver-response relationships for geomorphology, riparian vegetation, and fish disciplines. For fish, in low time allocation projects the responses were tightly centred around the median, whereas in projects with medium time allocations specialists likely accessed more nuanced information resulting in more detailed response curves. In contrast, macroinvertebrate responses were more sensitive for low time projects, possibly because these grouped more families into a single indicator and so needed to account for a wider range of responses. This also means that more time allocation does not directly mean that more water must be allocated to EFlows, at least in the case for invertebrates, as with additional time allocations actual requirements can be better understood and catered to.

Hydraulic indicators translate the underlying hydrology into ecologically meaningful parameters such as river depth, velocity and wetted area. Hydraulic and hydrodynamic models require much site-specific survey data across several seasons and often extensive modelling information. Subsequently, their outputs were found to be site- and species-specific. Links to hydraulic driving indicators require further translation back to hydrology through an understanding of the underlying models. The transferability of hydraulic driving indicators remains an avenue for future work as hydraulic information is recognized as an important driver in river ecosystems (Rice et al., 2010).

The driver-response relationships reviewed estimated response as a percentage of baseline abundance and do not comment on the actual abundance, which may indeed vary between different river systems and river types. For instance, Riseng et al. (2004) found order of magnitude differences in the abundance of algal and invertebrate biomass between hydrologically stable and flashy rivers, but similar responses to increased nutrient loadings in both systems. In studies where large amounts of field data are collected and analysed, it may be possible to calculate minor differences in the ecosystem response across river types for selected hydrological drivers, as shown by Bower et al. (2022). However, in the case of DRIFT and other ecosystem-based models (e.g., McManamay et al., 2013) that use relationships to predict future ecosystem response to change, there is an important recognition and calculation of uncertainty bands in these relationships (Brudvig and Catano, 2021). Subsequently, the resolution at which these studies managed data was more conservative in the shape of the response across different types of systems.

Although 12 of the study sites had non-perennial or flashy hydrology, this was a small subset of the 63 total sites and not sufficient to provide any firm conclusions regarding the transferability of the relationships that used the flood frequency as drivers, other than to note that these were used. The conclusions for the transferability of relationships between ecosystem components still holds for these sites; the limitation is that in addition to those indicators and relationships discussed, studies of non-perennial rivers must consider flood frequency, which is a major factor in determining the behaviour and response of non-perennial systems and this is not covered in the present study.

CONCLUSIONS

Driver-response relationships developed for EFlows assessments using the DRIFT method exhibit high spatial transferability across southern Africa, despite the wide range of specialist teams and time allocations used to set up each database. This supported the development of a generic library of indicators and driver-response relationships (Bukhari et al., 2024), from which indicators and driver-response relationships can be selected, and adjusted as needed, for EFlows assessments in the region. Adopting this approach would promote greater consistency in indicator and driver-response relationship selection and would further enhance the transferability of information generated, often at great cost, and build towards a knowledge base of driver-response relationships in southern Africa. Such a knowledge base would allow for more rapid, less expensive EFlows assessments and, importantly, facilitate entry by younger scientists to these kinds of studies. Lastly, the findings presented here, such as the long-term benefits of using well-defined frameworks when eliciting expert opinion, are applicable to other specialist led ecosystem-based models and approaches.

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AUTHOR CONTRIBUTIONS

H Bukhari: conceptualisation, methodology, data collection, analysis, writing of initial draft, revisions. A Joubert: methodology, data collection and analysis. C Brown: conceptualisation, supervision, reviews, and revision. K Esler: supervision and reviews.

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