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Biogeographic and β-diversity patterns for southern Africa's native freshwater fishes: a synthesis

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Abstract

Freshwater habitats are some of the most imperilled ecosystems in the world as they harbour numerous species threatened with extinction. In tropical Africa, acute deficiency of scientific data on the distribution patterns of freshwater biodiversity hampers successful conservation interventions. The number of newly described and resurrected freshwater fish species in southern Africa has increased considerably since the last bioregionalization effort, nearly three decades ago. Here, we utilize an updated matrix of catchment-scale native freshwater fish distributions to re-evaluate earlier biogeographic zonation patterns and examine the relative contribution of beta diversity to observed spatial distribution patterns in the subregion. Cluster analysis applied to an incidence data matrix of 259 native freshwater fish species from 17 drainage basins resulted in three major biogeographic zones, which generally corresponded to patterns shown in earlier studies. However, our analysis further revealed a split of the Eastern zone into two sub-clusters -- Northeast and Southeast. We decomposed the overall beta diversity (β_{SOR}), of southern Africa's native freshwater fishes into its nestedness (β_{SNE}) and turnover (β_{SIM}) components. In all three zones, the proportion of the nestedness resultant component (βratio) was less than 0.5, implying that the compositional variation in overall beta diversity was mainly driven by species turnover. The dominance of the turnover component to overall β-diversity suggests that conservation initiatives targeting multiple sites across broad spatial scales are likely to provide better outcomes for southern Africa's native ichthyofauna than a few large, protected areas. We discuss the relative contribution of environmental heterogeneity and dispersal limitation on observed bioregionalization and β-diversity patterns of native freshwater fishes in southern Africa. Incomplete knowledge of the taxonomic diversity of southern Africa's ichthyofauna affects the mapping of distribution patterns, stressing the need for increased sampling efforts, especially in high diversity drainages that border the Congo basin.

Highlights

- Quantitative analysis of fish distribution trends at the drainage basin level, and integration of recent taxonomic literature are necessary for a clear understanding of contemporary distribution patterns of southern Africa's freshwater fishes.

- We report new biogeographic zonation patterns at the basin level and examine underlying beta diversity components driving the observed spatial variability.

- Overall β-diversity was highest in the southern zone (β_{SOR}=0.84) compared to the eastern (β_{SOR}=0.66) and western (β_{SOR}=0.41) zones.

- Drainage basins in the Southern zone had the highest proportions of endemic species, while those in the Western zone had the highest overall richness.

- Our synthesis provides a new benchmark or baseline against which future progress can be measured and from which knowledge gaps can be identified and prioritized. Specifically, the design of freshwater protected areas in the subregion could benefit from fish distribution metrics obtained from this study.

Introduction

Africa's inland freshwater habitats are home to more than 3,000 fish species (Paugy et al. 2017), representing an enormous species diversity, inferior only to the Neotropics (> 5,000 species, Reis et al. 2003) among the major global ichthyofaunal biogeographic regions. Evidence on a global scale (Olden et al. 2010, Arthington et al. 2016, Reid et al. 2018, Dudgeon 2019) and for the African region (Stiassny 1996, Ogutu-Ohwayo and Balirwa, 2006; Snoeks et al. 2011) reveals increasing levels of anthropogenic induced threats to freshwater biodiversity, including habitat fragmentation, pollution, overfishing, invasive species, and climate change. Freshwater fishes are acutely susceptible to these threats due to their limited dispersal ability and constraints introduced by physical and saltwater barriers (Drakou et al. 2009, Filipe et al. 2009).

The magnitude of anthropogenic threats faced by freshwater biodiversity is often greater than the limited financial and technical resources available for conservation (Spector 2002), and that is especially true for developing tropical regions. Scientific studies that provide species distribution data useful in creating strategies that protect entire ecosystems as opposed to detailed data on individual species may therefore be more desirable if a significant proportion of threatened freshwater biodiversity is to be conserved. Global conservation strategies that are applied at larger spatial scales, such as the designation of protected areas, identification of biodiversity hotspots, and areas of high endemism, are dependent on our understanding of species distribution and bioregionalization patterns. Periodic updates on biogeographic zonation patterns are therefore important to evaluate the efficacy and representativity of current conservation strategies.

In recent decades, there has been renewed interest in updating biogeographic zonation patterns of freshwater fishes in different parts of the world, including China (Kang et al. 2014), Australia (Shelley et al. 2019), Argentina (López et al. 2008), and even global zones (Markovic et al. 2012, Pelayo-Villamil et al. 2015, Leroy et al. 2019). This upsurge in biogeographic revisions has been facilitated by the advent of new analytical tools (e.g. Kreft and Jetz 2010, Vilhena and Antonelli 2015, Edler et al. 2017) and the growing availability of new distribution data (e.g. Tedesco et al. 2017). Despite this documented rise in freshwater fish bioregionalization reviews elsewhere, distribution patterns on the African continent are still based on earlier data, which does not consider recent taxonomic revisions and newly described species.

Several early studies documented the biogeographical distributions of African freshwater fishes at the continental scale (e.g. Boulenger 1905, Pellegrin 1912, Poll 1957, Roberts 1975, Skelton 1988). Some of the foregoing bioregionalizations were done at coarse taxonomic scales such as family level (e.g. Roberts 1975, Skelton 1988). The seminal works of Jubb (1967) and Skelton (1993) provide the most recent descriptions of freshwater fish distributions with a focus on the southern Africa subregion. In his guide to fishes of the region, Skelton (1993) delimited three biogeographic zones within southern Africa (Zambezi, Karoo, and Cape). Today, however, it would be useful to have a more refined analysis suitable for implementing contemporary conservation strategies. The establishment of freshwater protected areas, for example, generally requires data on a much finer scale.

Furthermore, knowledge on the taxonomy and distribution of fishes in southern Africa has improved considerably since that most recent bioregionalization effort by Skelton (1993). That is a consequence of new field collections and monographs, and detailed taxonomic revisions of genera and families, which have all reported on new and resurrected species (summarized in Table S1). These developments have led to notable increases and refinements of available distributional data beyond those used in earlier bioregionalizations, underscoring the need for an updated synthesis of biogeographical distribution patterns of southern Africa's native freshwater fishes.

Beta diversity is an intrinsic component of biodiversity that measures species assemblage variation at different spatial and temporal scales (Dornelas et al. 2014). Overall beta diversity can be subdivided into two components – species turnover and nestedness (Baselga 2010, Baselga et al. 2017). The turnover component reflects the loss of and replacement of species between sites (Kang et al. 2018, Cai et al. 2019), while the nestedness component reflects monodirectional species loss without replacement between sites (Beca et al. 2017, Jiang et al. 2019). Decomposing β-diversity into its turnover and nestedness components is important for establishing the respective contribution of each component to the observed dissimilarity between communities (Kang et al. 2018). The resulting quantitative metrics have been used to guide management and conservation strategies at large spatial scales (Angeler 2013, Jiang et al. 2019). For example, where turnover is the dominant driver of β-diversity, this might indicate the presence of a high proportion of endemics, and the protection of several sites with variable species composition would be the most reasonable conservation option. In contrast, protecting a few sites with higher richness would be ideal where nestedness is the dominant component driving overall β-diversity patterns (Baselga, 2010, Fugère et al. 2016). In southern Africa, despite the importance of these metrics in informing conservation decisions, patterns of beta diversity for native freshwater fishes, including the quantitative contribution of decomposed components (turnover and nestedness), remain largely underexplored.

In the current study, we use multivariate approaches based on a comprehensive and updated incidence data matrix of native freshwater fishes from southern Africa to address the following objectives: 1) determine native freshwater fish similarity among southern Africa's major drainage basins, 2) provide a quantitative assessment of native freshwater fish biogeographic zonation patterns in the subregion, 3) quantify the relative contribution of overall beta diversity and its

      2

components (turnover and nestedness) in driving spatial distribution patterns of native ichthyofaunal assemblages in southern Africa's major drainage basins, and 4) analyze spatial distribution patterns of the most species-rich and endemic taxa in the subregion. This new information can guide aquatic resource managers in implementing conservation initiatives such as invasive species management and designation of freshwater protected areas at regional, basin, and sub-basin levels.

Materials and Methods

Study area

Species occurrence data were scored for 19 major drainage basins in southern Africa (Fig. 1). All basins in the subregion are part of two ichthyofaunal provinces in continental Africa (i.e. the Zambezi and Southern provinces; Snoeks et al. 2011). Major basins considered for this study either drain to the Indian Ocean on the

Figure 1. Inset: Delimitation of southern Africa on the continent; Main map: Major river drainage basins in southern Africa considered for the current study (*n* = 19). River basin abbreviations: CUN-Cunene, ETO-Etosha, OKA-Okavango, UPZ-Upper Zambezi, KAF-Kafue, MIZ-Middle Zambezi, LOZ-Lower Zambezi, SAV-Save, BUZ-Buzi, PUN-Pungwe, LIM-Limpopo, INC-Incomati, MAP-Maputo, UMB-Umbeluzi, TUG-Tugela, ORA-Orange, BER-Berg, OLI-Olifants, and SCB-South Coastal Basins. The green band marks the southern boundary of the Congo River Basin, the dashed line marks the northern boundary of the Lower Zambezi considered for this study (i.e. excluding the Lake Malawi basin and upper reaches of its discharge). The red band marks the ridge of the Great Escarpment along its southern and eastern extensions (west/northwest extensions not shown).

eastern and southern boundaries or the Atlantic Ocean on the western boundary of the subregion, with two exceptions – 1) the Okavango, an endorheic basin draining into the Okavango swamps in Botswana, and 2) the Cuvelai-Etosha (Etosha hereafter), a transboundary endorheic basin that drains several rivers flowing from Angolan highlands to the Etosha pan south of the Namibian border.

The Zambezi is the largest and longest (i.e. 2574 km) African river flowing to the Indian Ocean. It has undergone hydrological changes in its geological history that created topographic barriers along its course that demarcate four major sub-basins (i.e. Upper Zambezi, Kafue, Middle Zambezi and Lower Zambezi; Fig. 1). The Victoria Falls form the boundary between Upper Zambezi (upstream of the falls) and Middle Zambezi (below the falls), with an elevational drop of about 425 m between Victoria Falls and Lake Kariba. The Kafue River in Zambia also drops about 600 m through a steep gorge with waterfalls and rapids to its confluence with the Middle Zambezi. The Middle Zambezi stretches some 966 km from Victoria Falls through man-made Lake Kariba, past its confluence with the Kafue River and downstream to the Cahora Bassa rapids in Mozambique, which mark the eastern limit of the Middle Zambezi basin. That historically important rapids barrier is now largely flooded by a hydroelectric dam forming Lago de Cahora Bassa. The Middle Zambezi also has a major northern tributary, the Luangwa River, with a confluence at the Zambia-Mozambique border. The Lower Zambezi stretches about 580 km from just below Lago de Cahora Bassa (and dam) to the mouth of the Zambezi on the Indian Ocean (Fig.1).

Geographically, Lake Malawi (Fig. 1) is part of the Lower Zambezi system since it is connected via the Shire River, which drains from that lake into the Lower Zambezi in Mozambique just upriver from its mouth. Lower Shire River fish records were included in the Lower Zambezi presence-absence data. Fishes from Lake Malawi and its inflowing tributaries, in contrast, were not considered in this analysis because those systems harbour a unique ichthyofauna dominated by over 800 species of endemic cichlids (Snoeks 2004). Previous bioregionalizations (e.g. Jubb 1967, Skelton 1993) have also excluded fishes from the Lake Malawi basin as separate from the southern African ichthyofauna. Headwaters of the Upper Zambezi, Kafue, and Middle Zambezi/Luangwa drainages all interface with southern headwaters of the Congo basin (Fig. 1).

In the Southern ichthyological province, the Great Escarpment, a 5,000 km-long semi-continuous mountain range that stretches from north-western Angola through Namibia, South Africa, Lesotho, Eswatini and into eastern Zimbabwe (adjacent to Mozambique to the east; see Fig. 1 for southern and eastern extensions) is a major geomorphological feature strongly influencing hydrology of the Southern province (Clark et al. 2011). Almost all rivers in that region drain from different sections of the Great Escarpment. The largest river in the province (Orange),
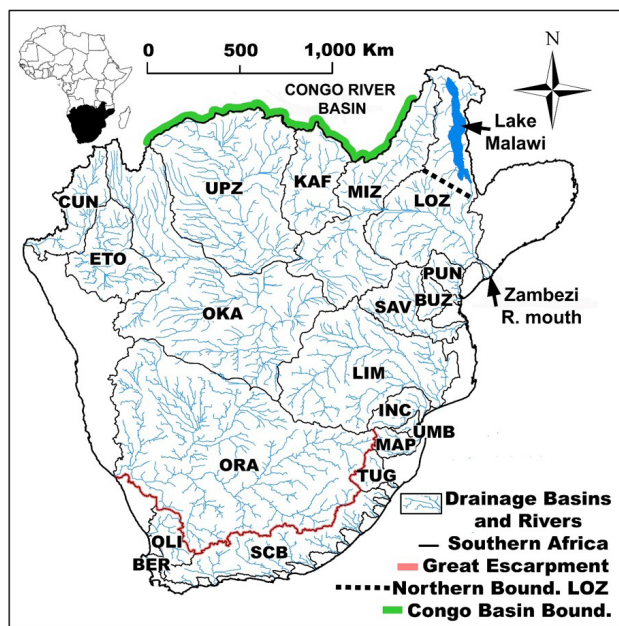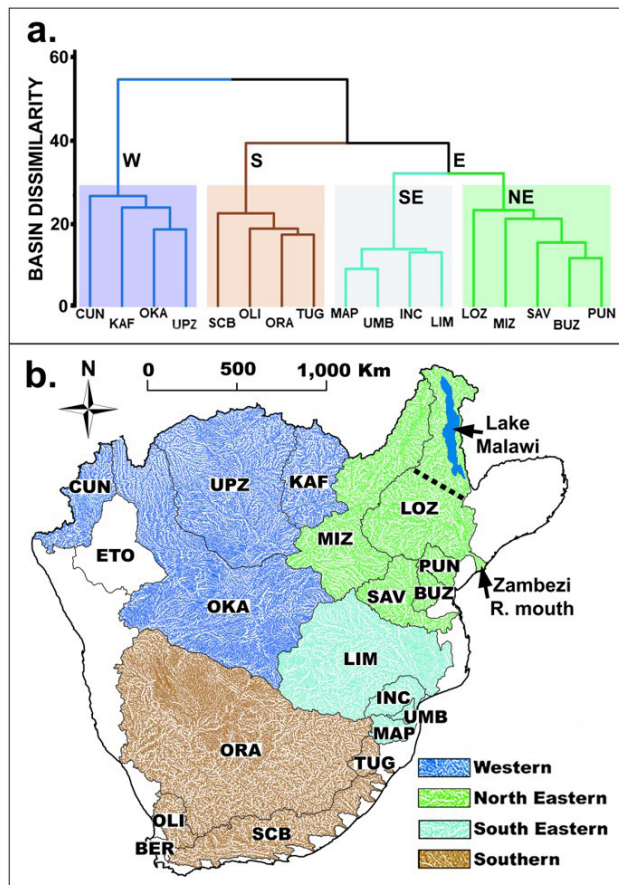
Figure 2. Biogeographic zonation of southern Africa's native freshwater fishes based on occurrences in 17 drainage basins: (a) Ward's minimum variance cluster dendrogram showing three major zones: Western (W), Southern (S), Eastern (E), and sub-clusters, North-Eastern (NE), and South-Eastern (SE); (b) map of geographical locations of the major clusters and sub-clusters in southern Africa.

has its source in the Drakensberg Mountains near the eastern coast (~ 150 km inland from the Indian Ocean) and flows ~ 1400 km south and then west to the Atlantic Ocean. Several smaller rivers drain from the escarpment and flow approximately perpendicular to the divide towards the Indian Ocean. For this study, eleven of these coastal rivers (i.e. Breede, Gourits, Gamtoos, Sundays, Fish, Kei, Mashe, Umzimvubu, Umgeni, Umkhomazi, and Umzingulu) located along the southern margin of the subregion, were grouped together as a single basin (i.e. South Coastal Basin). Previous studies (e.g. Chakona et al. 2013) have also grouped these river systems together as 'Southern Basins'.

Species presence-absence data

A total of 45 published sources on southern Africa's freshwater fish distributions, including species catalogues and primary literature were used to assemble an incidence (presence/absence) data matrix for 259 native freshwater fish species. Also included

were some museum records for Zambia (Bailey and Stewart, unpublished data). A full listing of the species presence-absence data and all references used to compile the matrix are provided in Tables S2a and S3.

Data were scored by recording species for their presence '1' or absence '0' in the 19 drainage basins. Most of the published sources used in creating the matrix were largely developed based on museum collections for which sampling effort was not uniform across drainage basins, and we acknowledge that some of the '0' values in the 'presence-absence' matrix, thus, may be due to insufficient sampling efforts. To minimize nomenclatural errors and update synonyms, all species names were normalized with Eschmeyer's Catalogue of Fishes (Fricke et al. 2020). Excluded from the analyses were: 1) introduced (from basins outside southern Africa) and translocated (from other basins in southern Africa) species (n = 24; Table S2b); 2) coastal and estuarine species that may enter freshwater, following the classification of Skelton (1993, 2001; n = 26; Table S2c); and 3) some morphotypes recognized in published accounts as likely to be new species but are not yet formally described.

Drainage clustering patterns

We evaluated biogeographic zonation patterns of southern Africa's native freshwater fishes using hierarchical clustering based on a Euclidean distance matrix and the Ward.D2 method (Murtagh and Legendre 2014). Clustering patterns were determined using the *'hclust'* function from the R package, *stats* (R Core Team 2021). Hierarchical clustering is an agglomerative dimension reduction method that iteratively groups objects with the shortest distance between them to produce results that can be visualized using dendrograms. To avoid bias in cluster estimation from the dendrogram output, we used an algorithmic approach (*NbCluster* package, Charrad et al. 2014) in R to determine the optimal number of clusters and the best partition of drainage basins into their respective clusters. We used canonical loadings and visual inspection of the incidence matrix to identify species with a greater contribution to cluster delimitation. In addition, ichthyofaunal relationships among the drainage basins were further explored using Principal Coordinate Analysis (PCoA) and a Bray-Curtis distance matrix. A One-Way Permutational Multivariate Analysis of Variance (PerMANOVA, Anderson 2001) with 9999 permutations was implemented in PAST (ver 4.05; Hammer et al. 2001) to test whether there were significant differences in compositional heterogeneity of fish assemblages across biogeographic clusters. Data from two basins, (i.e. Etosha, ETO, and Berg, BER) that had few native freshwater fish species (n < 10) were excluded from all multivariate analyses.

Beta diversity patterns

To compare the overall beta diversity for southern Africa's native freshwater fishes across biogeographic clusters, multiple site dissimilarities were calculated using the Sorenson's dissimilarity index (Baselga 2010). Comparable assessments of multiple site

dissimilarities across drainage basin clusters were made by computing average dissimilarity values using a resampling procedure, i.e. taking 150 samples drawn from four random sites in each cluster and computing the average using the *beta.sample* function in the R package *betapart* (Baselga and Orme 2012). Overall multiple site beta diversity (β_{SOR}) was further partitioned into two independent components — the turnover component (β_{SIM}) and the nestedness component (β_{SNE}) (Baselga 2010). To distinguish the major component driving overall beta-diversity patterns in the subregion, we obtained the relative contribution of the nestedness component using the equation: $\beta_{ratio}=\beta_{SNE}/\beta_{SOR.}$ Thus, $\beta_{ratio} < 0.5$ indicates that β-diversity is predominantly determined by species turnover, and $\beta_{ratio} > 0.5$ indicates nestedness as the dominant component (Dobrovolski et al. 2012). All maps were done in ArcGIS (ver 10.7).

Results

Biogeographic clusters

Output from the *NbClust* algorithm revealed that southern Africa's drainage basins can be partitioned into four clusters based on their composition of native freshwater fishes. The *NbClust* analysis further revealed the following best partition of southern Africa's drainage basins; *cluster 1* (OLI, ORA, TUG & SCB), *cluster 2* (INC, LIM, MAP & UMB), *cluster 3* (BUZ, PUN, SAV, MIZ & LOZ), and *cluster 4* (CUN, KAF, OKA & UPZ). We renamed the clusters to Western (W), Eastern (E) and Southern (S) zones, with the Eastern zone split into two sub-clusters – North-East (NE) and South-East (SE) (Fig. 2a, b). PCoA ordination of a Bray-Curtis distance matrix confirmed the clustering patterns (Fig. 3). A One-way Permutational Analysis of Variance (PerMANOVA) revealed that the cluster centroids for the four clusters were all significantly different in the ordination space (F=7.638; p=0.0001). In addition, pairwise comparisons of the four clusters showed significant differences among all the clusters (Bonferroni adj; p<0.05).

Dominant families and species characterizing biogeographic clusters

Dominant species of the Western zone

Four basins, (i.e. OKA, CUN, KAF and UPZ) clustered to form the Western zone (Fig. 2a, b). Canonical loadings and the incidence matrix showed that fish from nine families, including Cichlidae (*Serranochromis angusticeps, S. macrocephalus, S. jallae, S. thumbergi, Sargochromis carlottae,* and *Sa. giardi*); Clariidae (*Clarias stappersii* and *C. liocephalus*); Cyprinidae (*Coptostomobarbus wittei, Enteromius afrovernayi, E. barnardi,* and *E. fasciolatus*); Distichodontidae (*Nannocharax multifasciatus*); Mochokidae (*Synodontis macrostigma* and *S. macrostoma*); Mormyridae (*Mormyrus larceda* and *Pollimyrus castelnaui*); Mastacembelidae (*Mastacembelus frenatus*); Kneriidae (*Kneria polli*); and Alestidae (*Rhabdalestes maunensis*)
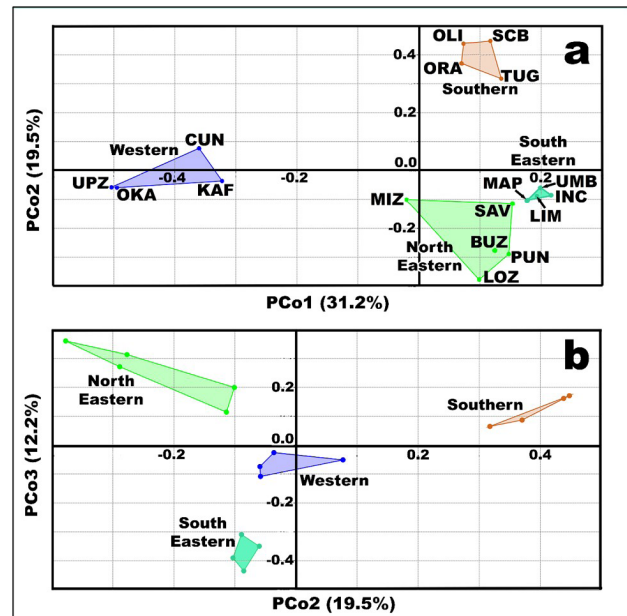

Figure 3. PCoA ordination of southern Africa's native freshwater fish occurrence data from 17 river basins showing separation of biogeographical zones between **a.** PCo1 and PCo2, and **b.** PCo2 and PCo3. Ordination was computed using Bray Curtis distance. Convex hulls group drainage basins that have similar fish assemblages and appear closer together in the orthogonal space. Percentage variation explained by the plotted principal coordinates is indicated on the axes. Abbreviations of drainage basin names are given on Fig. 1.

scored relatively higher values than other taxa. These 20 species were present in all or most of the Western zone's drainage basins, thus making important contributions to the delimitation of the cluster.

Dominant species of the Eastern zone

The Eastern cluster was composed of nine drainage basins split into two sub-clusters – North-East, NE, and South-East, SE. The NE sub-cluster (*n* = 5) was comprised of BUZ, PUN, SAV, MIZ, and LOZ drainage basins (Fig. 2a, b). Species from three families, including Mormyridae (*Mormyrus longirostris*); Malapteruridae (*M. shirensis*); and Cichlidae (*Oreochromis placidus*) were most important in delimiting the NE sub-cluster. The SE sub-cluster (*n* = 4) was comprised of INC, LIM, MAP and UMB drainage basins (Fig. 2a, b). Species from three families -- Mochokidae (*Chiloglanis paratus, C. swierstrai* and *C. pretoriae*), Cyprinidae (*Opsaridium peringueyi*), and Mormyridae (*Petrocephalus wesselsi*) -- made the greatest contributions to delimitation of the sub-cluster. Faunal similarities among these four drainages were relatively high compared to other clusters (Fig. 2a).

Dominant species of Southern zone

Four basins (OLI, ORA, TUG and SCB) clustered to form the Southern zone (Fig. 2a, b). Species from three families, including Cyprinidae (*Enteromius mandelai*

and *Labeo umbratus*); Galaxidae (*Galaxias zebratus*), and Clupeidae (*Gilchristella aestuaria*) scored relatively high on canonical loadings with presence in at least two or more basins (Table S2a). A total of 33 species from five families, including Cyprinidae (all 16 *Pseudobarbus* species, *Labeobarbus aeneus*, *L. kimberleyensis*, *Labeo capensis*, *L. rubromaculatus*, *L. seeberi*, *Enteromius amatolicus*, *E. cernuus*, *E. gurneyi*, *E. oraniensis* and *Namaquacypris hospes*); Anabantidae (*Sandelia capensis* and *S. bainsii*); Austroglanidae (*Austroglanis gilli*, *A. barnardi* and *A. sclateri*); Mormyridae (*Marcusenius caudisquamatus*), and Nothobranchidae (*Nothobranchius mkuziensis*) were all endemics restricted to only one of the four southern zone basins (Table S2a).

Richness patterns of five most dominant families

Patterns of richness data from five families with largest number of species (i.e., Cyprinidae, Cichlidae, Mochokidae, Mormyridae, and Amphiliidae) revealed a similar trend of decreasing richness along a north-south gradient (Fig. 4). Members of the Cyprinidae were present in all but one of the drainage basins considered for this study. Of the five major families selected for in-depth distribution analysis, cyprinids were the only group present in the three southernmost drainage basins -- BER, OLI and SCB (Fig. 4).

The Cichlidae were the second most widely distributed family in the southern African subregion, with representative species in 17 of the 19 drainage basins. The Amphiliidae and Mormyridae had a similar distribution pattern, being present in all basins except ETO, ORA,
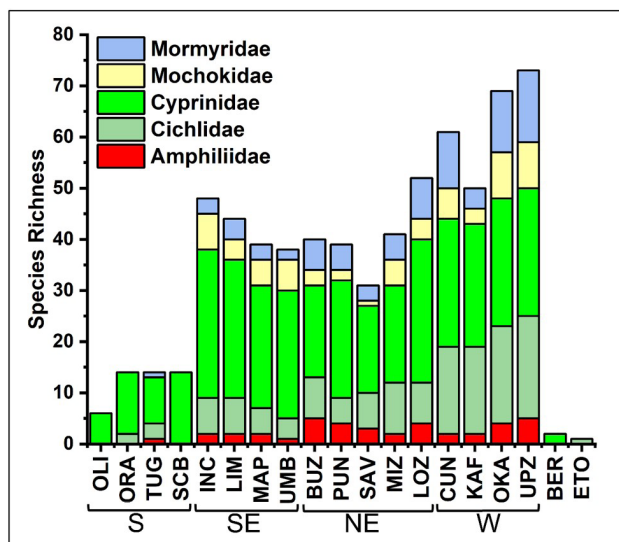
OLI, BER, and SCB. Members of the Mochokidae were present in all Western and Eastern zone drainage basins but were conspicuously absent from all Southern zone drainage basins (Fig. 4). Characteristic species within these and other less species-rich families, listed in the following sections (also, see Table S2a), help to explain the results of Ward's cluster analysis.

Beta diversity patterns

Multiple site dissimilarities across drainage basins in the subregion revealed that the overall beta diversity (β_{SOR}) and turnover-resultant component (β_{SIM}) were greater for native freshwater fish communities in Southern zone drainages (β_{SOR}=0.84; β_{SIM}=0.79) than Eastern zone (β_{SOR}=0.66; β_{SIM}=0.59) and Western zone (β_{SOR}=0.41; β_{SIM}=0.33) drainage basins (Fig. 5a & b). In

Figure 4. Stacked bar graph showing relative richness and distribution patterns for the five dominant fish families (i.e. Cichlidae, Mochokidae, Mormyridae, Amphiliidae, and Cyprinidae) with the highest number of species in the study area (i.e. *n* ≥ 10). Drainage basins are grouped by their zones from Cluster Analysis (Fig. 2a). Zone abbreviations: S = Southern, SE = South-Eastern, NE = North-Eastern, and W = Western; drainage basin codes are defined on Fig. 1.
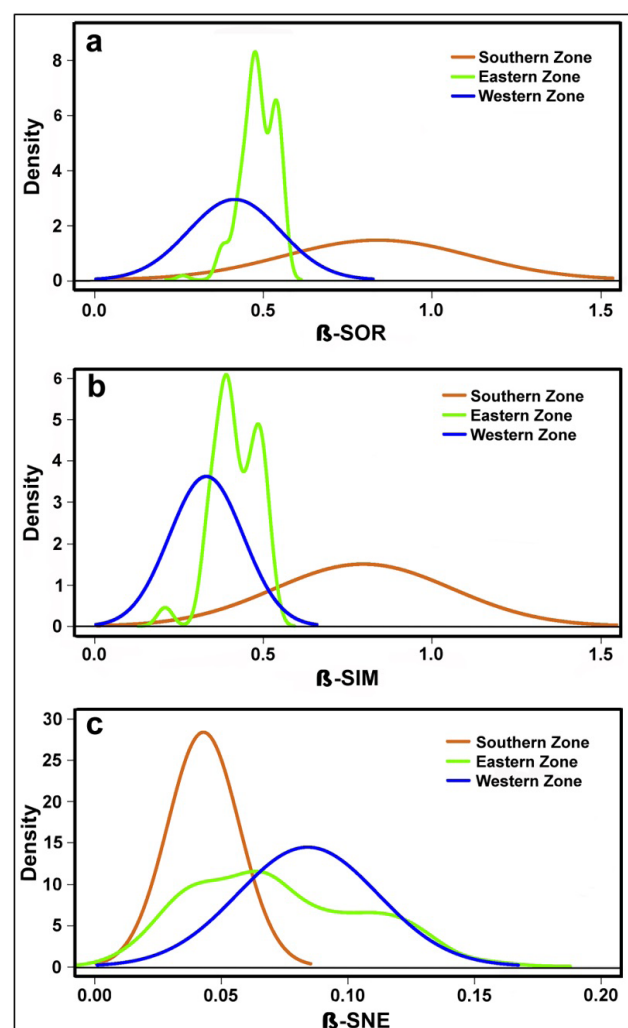

Figure 5. Frequency distribution of multiple site dissimilarities of native freshwater fishes in the three major biogeographic zones (Western, Eastern, and Southern) for (a) overall beta diversity, (β_{SOR}); with its turnover resultant, β_{SIM} (b); and nestedness resultant, β_{SNE} (c) components. Estimation of frequency distributions was achieved by a bootstrapping procedure with replacement of (*n* =150 samples) from four basins per biogeographic zone to calculate multiple site dissimilarities.

addition, the nestedness-resultant component was lower in Southern zone drainages (β_{SNE}=0.04) compared to Eastern (β_{SNE}=0.06) and Western zone (β_{SNE}=0.08) drainages (Fig. 5c).

In all three zones, the proportion of nestedness resultant component (β_{ratio}) was lower than 0.5, i.e., β_{ratio}=0.05, 0.1, and 0.2 for Southern, Eastern and Western zones, respectively, indicating that the compositional variation in overall beta diversity for southern Africa's major drainage basins (β_{SOR}) was mainly driven by the turnover resultant component, (β_{SIM}) (Fig. 6).

Discussion

Biogeographic zonation patterns

The current understanding of biogeographical zonation patterns of freshwater fish in southern Africa identifies two major ichthyographic provinces, a tropical Zambezian province and a temperate Southern province (Skelton 1993, Snoeks et al. 2011, Snoeks and Getahun 2013). Skelton (1993, 2001) further subdivides the latter into the Karoo group (predominantly comprised of fishes of the Orange River basin) and the Cape group (comprised of fishes restricted to rivers of the Cape Fold Mountains). Formation of those major ichthyofaunal provinces (Zambezian and Southern) is considered to have been a result of two progressive waves of fish invasions from northern parts of the African continent in the mid and late Pliocene (Skelton 1993, 2001). An alternative proposal for the origin and distribution of southern Africa's freshwater fishes are evolutionary arenas (Skelton 1993, 2001). The evolutionary arenas correspond to three ichthyofaunal areas in the subregion (Western, Eastern and Southern) from which southern Africa's freshwater fishes might have been derived.
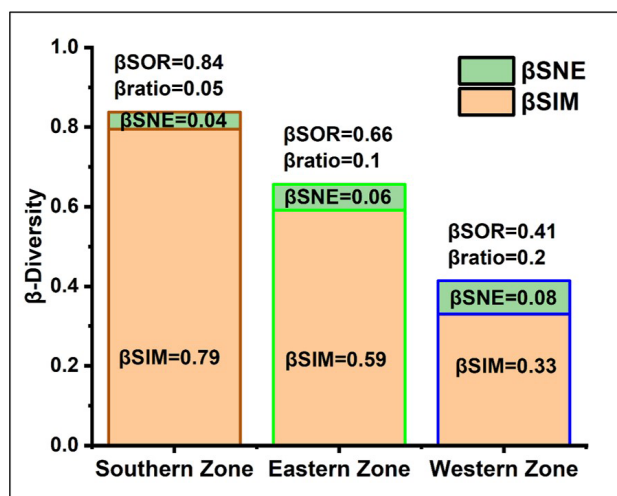

Figure 6. Multiple site Sorensen dissimilarity index (β_{SOR}), with its turnover (β_{SIM}) and nestedness (β_{SNE}) components for southern Africa's native freshwater fishes. βratio indicates the ratio between β_{SNE} and β_{SOR}.

Clustering patterns from our analyses (based on native freshwater fishes only) revealed the presence of four biogeographic zones or clusters -- Western, Eastern (with two subzones) and Southern -- within the subregion (Fig. 2a, b). Although our clustering patterns did not distinguish between Skelton's 'Karoo' and 'Cape' groups of the Southern province, our biogeographic zones corroborate the 'evolutionary arenas' that he previously proposed (Skelton 1993, 2001). However, we show a split of the Eastern zone to form the North-Eastern and South-Eastern subzones. Our results further complement the 'evolutionery arena' proposal by providing additional insights into the level of similarity among drainage basins within each zone and highlighting some of the major taxonomic groups whose distribution patterns contributed significantly to the delimitation of the clusters (Table S2a). In addition, we provide a detailed discussion below on how observed biogeographic patterns were likely influenced by geomorphological (Moore 1999, Moore et al. 2012, Stankiewicz and de Wit 2005a, Stankiewicz and de Wit 2005b), hydrographic (Jubb 1964, Balon 1974, Roberts 1975, Bishop, 1995), topographic (Kramer and Van der Bank 2011), climatic (Kottek et al. 2006), and evolutionary (Joyce et al. 2005, Day et al. 2009, Van Steenberge et al. 2020) patterns and processes operating at different spatial and temporal scales in the subregion.

Western zone

Intra-zonal grouping patterns revealed that OKA and UPZ have more species in common compared to the other two basins in this zone (Fig. 2a), a result consistent with findings on drainage basin similarity for Namibian river systems (Hay et al. 1999). The hydrographic history of the Zambezi basin provides evidence that the UPZ was a separate basin from the MIZ and LOZ during the Pliocene and flowed south into the now extinct Makgadikgadi Lake (Balon 1974, Moore et al. 2012). The drainage evolution model of the region (Moore et al. 2012), largely ascribes tectonic processes as the principal driver of hydrographic rearrangements along the Zambezi that led to the formation of Makgadikgadi. The diversion of the UPZ into the Makgadikgadi basin is thought to have been a result of a tectonic uplift of the Chobe Horst across the Zambezi (Moore et al. 2012). The contraction and extinction of the paleo-lake are thought to have been caused by a combination of river captures that reduced inflow into the lake (Moore et al. 2012) and a tectonic upwarp in the Mid-Pleistocene that eventually diverted waters of the UPZ to flow in the easterly direction towards MIZ (Balon 1974). There is also evidence that during periods of heavy flooding, the Okavango River system may temporarily link to the Upper Zambezi via the Chobe swamps (Jubb 1967). The foregoing historical links and hydrographic processes, potentially, could have allowed exchange of species between the UPZ and OKA basins, and that could explain, in part, the high similarity of fish assemblages between them.

Interestingly, despite being a tributary of the MIZ located in the Eastern zone, KAF grouped with CUN

from the Western zone (Fig. 2a). A possible explanation for this grouping pattern could be the presence of Kafue gorge. That stretch of steep rapids and waterfalls on the lower Kafue likely inhibits the upstream dispersal of MIZ fishes despite their geographic proximity and flow connectivity. Natural topographic features such as waterfalls have been shown to affect fish migration and connectivity of freshwater systems (Balon and Stewart 1983, McPhail and Lindsey 1986, Torrente-Vilara et al. 2011).

The dominance of haplochromine cichlids (i.e. the genera *Serranochromis* and *Sargochromis*) on canonical loadings for the Western zone is corroborated by phylogeographic evidence (e.g. Joyce et al. 2005), which suggests that these riverine cichlids are products of a recent adaptive radiation in the paleo-lake Makgadikgadi, which dried up in the Holocene. That previously huge lake (i.e. ~120,000 km^2) formed during the Pleistocene in the northern Kalahari Desert is thought to have been the source of haplochromine cichlids that seeded nearly all the southern African drainage basins (Joyce et al. 2005). For example, serranochromine cichlids are relatively more abundant in the UPZ, OKA, KAF and CUN basins than they are in the MIZ (Table S2a), a pattern reflecting their importance in clustering of these basins to form the Western zone. Like serranochromine cichlids, distribution patterns of *Synodontis* catfishes, which also made a greater contribution to cluster delimitation for this zone, are likewise thought to have been influenced by adaptive radiation in the paleo-lake Makgadikgadi (Day et al. 2009).

Similarities of fish assemblages in Western zone basins also have been attributed to river capture (Poll 1967, Skelton 1993, Hay et al. 1999, Bills and Marshall 2004, Darwall et al. 2009), a drainage rearrangement process in which a river undergoing aggressive headward erosion diverts the flow of an adjacent river to its own riverbed (Bishop 1995). The geographic proximity of Congo and Zambezi ichthyofaunal provinces (Roberts 1975, Snoeks et al. 2011) could have facilitated faunal exchanges via river captures between headwater tributaries of the Zambezi River and southern tributaries of the Congo basin (Fig. 1). For example, the clariids *Clarius stappersii* and *C. liocephalus*, which had high scores on canonical loadings for the Western zone, also have natural distributions covering much of the Congo basin (Agnese and Teugels 2005). Their presence in Western zone basins, which marks the southernmost extent of their range, is likely to have been facilitated by river capture.

Eastern zone

Topographic and climatic factors play a greater role in delimiting this zone through their influence on fish distribution patterns. For the North-Eastern section, for example, the Victoria Falls and Kafue Gorge are barriers that apparently prevent upstream and might inhibit downstream migration of fishes between the Eastern zone's MIZ basin and Western zone basins (i.e. UPZ and KAF). The role of these topographic barriers

has been confirmed by previous studies (e.g. Jackson 1961, Jubb 1967, Bell-Cross 1972, Kramer and van der Bank 2011) that have consistently shown that the MIZ is relatively poor in species richness compared to the UPZ and KAF. Although there is literature that minimizes the role of the Victoria Falls as a biogeographical barrier (see Balon 1974), citing the presence of species otherwise distinct to the UPZ below the falls, this has been disputed by recent studies (e.g. Kramer and van der Bank, 2011, Marshall 2011). In fact, several factors can explain the presence of UPZ fishes below the falls including: 1. they could have reached the MIZ via the Victoria Falls hydroelectric power station; 2. they could have been translocated during stocking programs soon after the completion of Kariba dam; or 3. they were already present in the MIZ before construction of the dam as there was relatively little information about the region's ichthyofauna except for brief surveys conducted from 1960-1961. Whatever the variables responsible, it remains untested that fish can survive the drop over the Victoria Falls, and the latter remains a major barrier separating UPZ and MIZ ichthyofaunal assemblages. In addition, the transition of vegetation types from wet savanna in the higher altitude Western zone to a dry savanna biome in the lower altitude Eastern zone (UNEP 2008), could also represent an ecological gradient influencing the biogeographic break between fish assemblages of the Eastern and Western zones in the subregion.

As noted in the description of the study area (under Materials and Methods, above), the Zambezi River downstream from Victoria Falls has been influenced by two large hydroelectric developments, forming Lake Kariba in the MIZ and Lago de Cahora Bassa at the boundary between the MIZ and LOZ. These lakes have flooded considerable fluvial habitat and fragmented the river system, blocking nearly all fish migrations that might have previously gone past those dam sites. The extent to which these dams might have compromised diversity of fluvial fishes in these river reaches is largely unknown. A third hydropower project has already reached implementation stage in the Batoka Gorge, 54 km downstream from Victoria Falls and upstream from Lake Kariba, converting more fluvial to lacustrine habitat and further fragmenting this ecosystem (AUDA-NEPAD 2019). Given our poor knowledge of fishes inhabiting such high gradient river reaches, it would seem both urgent and interesting to conduct post-impoundment studies on species diversity and abundance of those fish communities and compare results to available data from pre-impoundment surveys. Such data would provide valuable guidance to conservationists and fisheries managers evaluating the impact of future hydro projects on fishes of the Zambezi.

The north-south split between the two eastern subclusters (NE and SE) has recently been corroborated with phylogeographic studies in the region. Using DNA sequences of the mitochondrial *cytochrome b* gene region of a widely distributed species of catfish, (*Clarias gariepinus* Burchell, 1822), Van Steenberge et al. (2020) found that populations from the Zambezi ichthyofaunal

province (*sensu* Skelton 1993) were subdivided into western, central, and eastern sectors. Those are the same assemblage clustering zones observed in this study (Fig. 2a), except that, based on genetics of that species, the MIZ population clustered most closely with the SE rather than the NE population. In addition, climatic factors such as temperature and precipitation, both of which are notably lower in SE compared to NE basins, also can be influencing the split. Apart from the MIZ, drainage basins in the NE subcluster are part of the Eastern Highlands Zimbabwe freshwater ecoregion (Abell et al. 2008), which is characterized by high rainfall and rich floral diversity, including Afromontane evergreen forests and miombo woodlands (Timberlake et al. 2020). In addition, the region harbours some endemic, range-restricted fishes such as *Labeobarbus pungweensis* (Jubb 1967). As with MIZ and LOZ, fluvial habitats in the SAV basin have been disrupted by construction of the Tokwe-Mukosi dam, commissioned in 2017. The resulting reservoir, with a total volume of 1.8 billion m^3 at full capacity and a surface area of 9640 ha (Mhlanga et al. 2020), is the largest inland water body in Zimbabwe. PUN and BUZ drainages, which showed a high similarity coefficient in the NE sub-cluster (Fig. 2a), are thought to link to the LOZ basin along the coastal plains during periods of heavy rainfall and flooding, enabling the exchange of fishes among those basins (Darwall et al. 2009).

In the SE subcluster, a lower mean annual precipitation and mean annual temperature compared to the NE subcluster could have influenced reductions in species richness and increased differences between the two subclusters. Also, apart from the LIM drainage, basin sizes in this zone are small and main rivers in this subcluster flow only short distances to reach the Indian Ocean. Members of the genus *Chiloglanis*, which recorded high canonical values for this subcluster, are common in most basins, with a few endemic species such as *Chiloglanis anoterus* and *C. bifurcus* restricted to headwaters of the INC basin (Skelton 1993).

Southern zone

In the Southern zone, altitudinal variation over short distances caused by the Cape Fold Mountains, and a drop in surface and water temperature from the ORA basin to coastal drainages on the southern coast are factors partly responsible for the clustering patterns and low species richness observed for basins in this zone. Studies on southern Africa's fish species richness in coastal marine habitats (Turpie et al. 2000) and natural freshwater lakes (Whitfield et al. 2017), have observed a similar trend (i.e. decreasing species richness from warm tropical towards cool temperate areas of the subregion). That trend, however, also involves replacements by fishes physiologically adapted to cooler waters, so beta diversity of the Southern region is dominated by turnover (β_{SIM}, Fig. 6).

There was little overlap in distribution ranges of fish assemblages across the four basins in the Southern zone. The relatively moderate similarity among basins in this zone reflects the large number of endemic species within each drainage basin (Fig. 7).
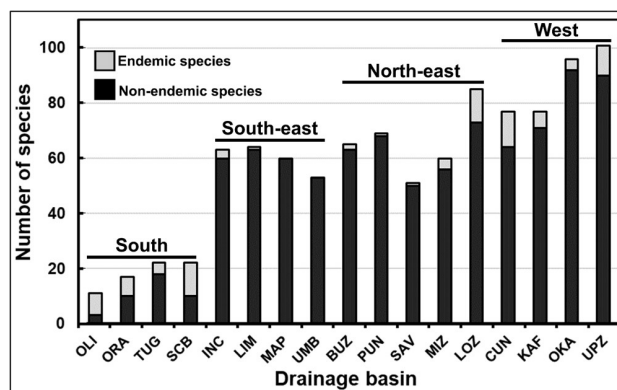

Figure 7. Comparisons of numbers of endemic and non-endemic fish species in 17 drainage basins of southern Africa, organized by four biogeographic zones illustrated in Fig. 2. Drainage basin codes follow those defined in Fig. 1.

Several studies (e.g. Jubb 1964, Roberts 1975, Skelton 1993, Darwall et al. 2009, Ellender et al. 2017, Whitfield et al. 2017) have reported a high proportion of localized endemics in this zone, predominantly involving members of the family Cyprinidae. In addition to marked changes in climatic conditions from subtropical to temperate (Kottek et al. 2006), geomorphological factors such as the Great Escarpment, a highland arc that stretches from the Atlantic coast near Namibia to the east coast near Mozambique, and the Cape Fold, an exhumed belt of folded Paleozoic mountains (Stankiewicz and de Wit 2005a), are important topographic features responsible for allopatric differentiations of species forming the distinct ichthyofauna of this region. Furthermore, coastal flowing rivers such as those in the SCB and OLI are often deeply incised with limited opportunities for lateral transfer of fish. The presence of these natural isolating geomorphological features over time could have promoted independent evolutionary pathways of fish faunas, leading to high endemism in the Southern zone. In recent times, fluvial habitats of the Orange River have been disrupted by two major hydroelectric projects, the Gariep and Vanderkloof dams, with likely negative effects on fluvial fishes of the flooded reaches.

Family dominance patterns

Analysis of a subset of the five most species-rich families (Fig. 4) showed that only the Cyprinidae covered 18 of the 19 drainage basins assessed in this study, including being the only native freshwater fish family present in all four of the Southern zone basins. Cyprinids are Ostariophysi, a superorder of fishes that dominates most freshwater habitats worldwide (i.e. 64% of global freshwater species; Helfman et al. 1997). In Africa, cyprinids have a pan-African distribution (Skelton et al. 1991) and are a major component of the freshwater ichthyofauna, being exceeded in overall species richness only by the Cichlidae. The latter is exceptional in having undergone numerous waves of explosive speciation in the East African Great Lakes (Schluter 2000, Salzburger et al. 2014), including Lake

Malawi in the LOZ drainage. Members of the dominant cyprinid genus in southern Africa's coastal basins (i.e. *Pseudobarbus*), show a vicariant distribution consistent with the hydrogeographic history of the region (Skelton et al. 1991). In addition, African cyprinids show certain attributes like phenotypic plasticity, omnivorous feeding, and broad tolerance to diverse riverine and lacustrine habitats (Skelton et al. 1991) that might explain their dominance in all southern Africa's drainage basins, except in ETO.

The families Cyprinidae, Amphiliidae and Mormyridae have received more taxonomic attention in the subregion since the last bioregionalization by Skelton (1993). Recent taxonomic revisions have contributed to the discovery of a disproportionate number of new species in these families (Table S1). For example, molecular approaches and electric organ discharge patterns, have both increased our understanding of and augmented the number of species in several mormyrid genera, including *Hippopotamyrus* (Kramer et al. 2004, Kramer and Swartz 2010)*, Marcusenius* (Maake et al. 2014, Kramer et al. 2016), *Petrocephalus* (Kramer and Van Der Bank 2000, Kramer et al. 2012) and *Pollimyrus* (Kramer et al. 2003, Kramer et al. 2014). In the Amphiliidae, morphological variation has been used to revise the genus *Zaireichthys*, leading to the description of six new species, (Eccles et al. 2011). More recently, Mazungula and Chakona (2021) used molecular and morphological approaches to describe four new species in the genus *Amphilius* (Table S1). In the Cyprinidae, both morphological and molecular phylogeographic techniques (e.g. Chakona et al. 2014, Chakona and Skelton 2017, Kambikambi et al. 2021) have been applied in describing new species in the genera *Enteromius, Labeobarbus*, *Pseudobarbus,* and *Opsaridium* (Table S1). The distribution patterns of the five families also reveal the demarcation between the Zambezian and Southern ichthyological provinces (Snoeks et al. 2011). Except for the Cyprinidae, there is a sharp decrease in species richness for most of the major families in drainage basins south of the TUG basin (Fig. 4), making that drainage the southernmost extent for most of the Zambezian fauna in the subregion.

Beta diversity patterns

The turnover component of beta diversity (β_{SIM}) was the principal driver of overall beta diversity patterns for native freshwater fishes in southern Africa's major drainage basins (Fig. 6). At broad spatial scales, environmental filtering and dispersal limitation have been observed to be among the major mechanisms influencing overall beta diversity patterns (Freestone and Inouye 2006, Barton et al. 2013). Environmental filtering is often promoted by the presence of environmental constraints that favor niche differentiation, speciation, and ultimately species turnover across broad spatial scales (Heino et al. 2013). Similarly, dispersal limitation is associated with colonization, extinction, and speciation processes that drive spatial turnover across biological communities

(Zeni et al. 2020). Turnover and nestedness patterns obtained from our analysis support the occurrence of these two major processes in southern Africa's major drainage basins. For example, the overall beta diversity (β_{SOR}) was higher in the Southern zone (β_{SOR}=0.84) compared to the Eastern (β_{SOR}=0.66) and Western (β_{SOR}=0.41) zones (Figs. 5, 6). Most of the basins in the Southern zone are part of the Cape Fold Mountain Aquatic Ecoregion (Skelton 1993) where resident fishes include a high proportion of geographic range-restricted endemics (Skelton 1986, Wilshart and Day 2002, Tweddle et al. 2009, Ellender et al. 2017, Chakona et al. 2018). Except for a few cases where phylogeographic evidence has demonstrated gene transfers among isolated basins (e.g. Chakona et al. 2013, Chakona, et al. 2015), most species in this region are restricted to single river systems (Chakona et al. 2015). Geographical isolation is promoted by deeply incised river valleys that have historically prevented lateral exchanges of native freshwater fishes, leading to high levels of endemicity (Ellender et al. 2017). Although basins in this region have low species richness compared to Western and Eastern drainage basins (Fig. 7), their high levels of endemic species and limited habitat should give them proportionately more attention in regional conservation planning.

Conclusions and Conservation Implications

Results from this first multivariate analysis of southern Africa's native freshwater fish distributions improve upon previous understandings of broad-scale biogeographic patterns in the subregion. Though our bioregionalization patterns show a general agreement with previous work (e.g. Skelton 1993), results provide new perspectives on intra-zonal similarity patterns among drainage basins. Such perspectives can be used in management and conservation initiatives, including restoration projects and regulation of introduced and invasive species at basin and sub-basin levels. Furthermore, the biogeographic zonation patterns presented here are based on an updated native freshwater fish distribution data matrix for the subregion (Table S2a), which is enhanced compared to information available for previous bioregionalization studies. This synthesis, thus, provides a new benchmark or baseline against which future progress can be measured and from which knowledge gaps can be identified and prioritized for future research programs.

Only 44 new species have been formally described in southern Africa for the 28-year period (1993–2021) since the most recent bioregionalization (Table S1), and of those, 14 are from one family, Mormyridae. The low discovery rate of new species in this subregion points to limited active research in faunal surveys and related studies in systematic ichthyology for countries north of South Africa; many of those areas remain poorly documented or unexplored. New explorations in the high diversity drainages that border on the Congo basin (Fig. 1) are especially likely to yield many new species. In the Western zone, numbers of endemic species per

basin are like what one finds in the Southern zone, but those Western endemics comprise relatively smaller proportions of total assemblages (Table S2a, Fig. 7).

More recently, taxonomic work on ichthyofaunas of the Cape Fold Freshwater Ecoregion (Ellender et al. 2017), the Eastern Zimbabwe Highlands Freshwater Ecoregion (Chakona et al. 2018) and several drainage basins in southern Africa (Mutizwa et al. 2021), have all revealed the presence of species complexes and previously unrecognized diversity in several genera, including *Hippopotamyrus, Galaxias, Pseudobarbus, Sandelia, Amphilius, Zaireichthys* and *Chiloglanis*. Similarly, molecular phylogeny studies have exposed previously unrecognized diversity in the cyprinid genus *Enteromius* (Schmidt et al. 2017, Van Ginneken et al. 2017). These examples of cryptic and underexplored diversity highlight the need and likely benefits of taxonomic reviews of the over 50 genera that remain less studied in southern Africa (Table S2a). Incomplete knowledge of taxonomic diversity in this subregion may affect the mapping of distribution patterns and compromise effective conservation of the region's native freshwater fishes. Ignorance of a species' presence often may be a threat to its survival.

In addition, an improved understanding of relationships among distribution and endemism patterns can be important in designing and implementing targeted action to mitigate human-induced threats to freshwater fish resources in the subregion. For example, based on these patterns, resource managers can make models for selecting suitable areas to establish specially designed freshwater protected areas. Inland freshwater ecosystems in the subregion are poorly represented within the existing protected area framework. Most of the protected areas primarily were designed for conserving terrestrial biodiversity. Several studies have questioned the efficacy of terrestrial protected areas in conserving freshwater biodiversity (e.g. Chessman 2013, Azevedo-Santos et al. 2018) because they do not account for fluvial connectivity of freshwater ecosystems.

Compared to most countries in the subregion, South Africa has made considerable progress in implementing frameworks that recognize freshwater features as conservation priorities. Freshwater-specific conservation efforts in South Africa started with experts identifying sites of conservation importance in the early 1970's (Noble 1974) and have been refined over the years to the current Freshwater Ecosystem Priority Areas (FEPAs) (Nel et al. 2011). FEPAs identify spatial priority areas for conserving freshwater systems such as rivers, wetlands, and estuaries to maintain key ecological processes, ecosystem types, and freshwater biodiversity (Nel et al. 2011). To date, FEPAs cover 22% of South Africa's river length, 38% of wetland areas, and 41% of estuaries (Roux and Nel 2013). Given the high endemicity patterns of freshwater fishes in the Southern zone, initiatives such as FEPA will likely provide the much-needed safety net for the conservation of endemic species. For maximum impact, however, such initiatives will need to be replicated elsewhere in the subregion, especially to the north. In addition, most drainage basins in the subregion transcend one or more national boundaries (e.g. Zambezi, Limpopo, Buzi, Pungwe, Etosha and Okavango). The transboundary nature of these lotic systems requires regional cooperation as human activities in unprotected headwaters of a river basin may affect conservation efforts on the lower reaches of that same basin in a different country.

Partitioning and quantifying the contributions of nestedness (β_{SNE}) and turnover (β_{SIM}) to overall beta diversity (β_{SOR}) provides important information for the conservation and management of aquatic biodiversity (Angeler 2013, Jiang et al. 2019). When nestedness is the major determinant of overall beta diversity, protecting a few sites with higher richness would be a reasonable strategy to maintain overall diversity. In contrast, the dominance of turnover to overall beta diversity suggests that conservation programs should target multiple sites over large spatial areas to conserve the overall diversity. In this regard, the dominance of the turnover resultant component in southern Africa's native freshwater ichthyofauna (Fig. 6) implies that conservation initiatives targeting multiple sites across broad spatial scales in the subregion are likely to provide better conservation outcomes than establishing a few large, protected areas.

The availability of new and geo-referenced distribution data in the future likely will lead to the refinement of patterns presented here. Specifically, boundaries between biogeographic zones are not always abrupt as depicted in our maps; instead, they may be characterized by transition zones, which are difficult to map using incidence data alone. Special consideration should be given to local, endemic taxa that may be vulnerable to extinction because of their low abundance and limited habitat, important criteria in species conservation assessments (IUCN 2019). In general, more attention should be given to taxonomic and phylogeographic studies on the ichthyofauna of southern Africa to facilitate deeper evolutionary interpretations that can be used to guide conservation planning.

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Author Contributions

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Table S1. Newly described (N) and resurrected (R) native freshwater fish species in southern Africa since the last bioregionalization by Skelton (1993).
Table S2a. Presence-Absence data for native freshwater fishes from 19 drainage basins in southern Africa and associated literature references.
Table S2b. Incidence matrix for freshwater fish species introduced to various river basins in southern Africa from outside the region and associated literature references.
Table S2c. Incidence matrix for coastal estuarine fish species that enter fresh or brackish waters of southern Africa and associated literature references.
Table S3. Table S3. Numbered references for new or resurrected species and distribution records listed in Tables S1 and S2a,b,c.

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