

## RESEARCH ARTICLE

# Vulnerability of Cape Fold Ecoregion freshwater fishes to climate change and other human impacts

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## Abstract

1. Native freshwater fish populations throughout South Africa's Cape Fold Ecoregion (CFE) are in decline as a result of human impacts on aquatic habitats, including the introduction of non-native freshwater fishes. Climate change may be further accelerating declines of many species, although this has not yet been studied in the CFE. This situation presents a major conservation challenge that requires assigning management priorities through assessing species in terms of their vulnerability to climate change.
2. One factor hindering reliable vulnerability assessments and the concurrent development of effective conservation strategies is limited knowledge of the biology and population status of many species. This paper reports on a study employing a rapid assessment method used in the USA, designed to capitalize on available expert knowledge to supplement existing empirical data, to determine the relative vulnerabilities of different species to climate change and other human impacts. Eight local freshwater fish experts conducted vulnerability assessments on 20 native and 17 non-native freshwater fish species present in the CFE.
3. Results show (1) that native species were generally classified as being more vulnerable to extinction than were non-native species, (2) that the climate change impacts are expected to increase the vulnerability of most native, and some non-native, species, (3) that vulnerability hotspots requiring urgent conservation attention occur in the Olifants-Doring, upper Berg and upper Breede River catchments in the south west of the region, (4) that in addition to providing guidance for prioritizing management interventions, this study highlights the need for reliable data on the biology and distribution of many CFE freshwater fishes, and (5) that identification of priority areas for protection should be based on multiple sources of data.

## KEYWORDS

alien species, catchment, climate change, conservation evaluation, endangered species, fish, river

## 1 | INTRODUCTION

The Cape Fold Ecoregion (hereafter CFE) of South Africa is one of the five aquatic ecoregions of Southern Africa and incorporates the drainages that flow off the Cape Fold Mountains along the southern fringe of the African continent (Abell et al., 2008). Although the area is best known for the vascular plant diversity and endemism of the Cape Floristic Region, the CFE is home to an assemblage of range-restricted endemic freshwater fishes, the majority of which are high

conservation priorities and are under severe threat of extinction (Ellender, Wasserman, Chakona, Skelton, & Weyl, 2017). The freshwater fish fauna of the CFE is characterized by low species diversity (23 species), and high endemism (20 species) (Ellender et al., 2017). Fourteen of the 20 fishes endemic to the CFE are currently evaluated as Vulnerable, Endangered or Critically Endangered using International Union for Conservation of Nature (IUCN) Red-List criteria (Chakona, Chakona, & Swartz, in press; Tweddle et al., 2009; Weyl, Finlayson, Impson, Woodford, & Steinkjer, 2014). Human-induced degradation

of aquatic habitats, including the introduction of non-native freshwater fishes (i.e. introduced to South Africa), water abstraction and habitat degradation, has resulted in dramatic decreases in the distribution, range and abundance of many of these species over the last century (Tweddle et al., 2009). To compound matters, recent biogeographic and taxonomic research in the CFE using molecular techniques has revealed that diversity has been severely underestimated. The consequence is that species previously thought of as widespread are now being split into species complexes consisting of a number of genetically unique lineages, many of which are limited to single systems, streams or reaches of streams (Ellender et al., 2017). While research on the detrimental impacts of non-native fishes and habitat degradation on native fish assemblages has been undertaken, the recently recognized threat of climate change has not been evaluated.

Predictions for the CFE include significant increases in water temperature and decreased total runoff over the next 50 years (Dallas, 2013; Dallas & Rivers-Moore, 2014; Hewitson, Tadross, & Jack, 2005). Decreased river flows and increased water temperatures are likely to increase the risk of extinction for the remnant populations of native fishes which are already highly fragmented (Clark, Impson, & Rall, 2009; De Moor & Day, 2013). For example, analyses of distributions for 32 stream fishes in France indicated a general trend of distributional shifts upstream to higher elevations in response to increasing temperatures downstream (Comte & Grenouillet, 2013). These distributional shifts would not be possible for many species in the CFE owing to instream physical barriers (waterfalls, damming, abstraction causing stream drying) and/or biological barriers (non-native fishes) confining populations.

The constrained distributions of CFE native fishes presents a major conservation challenge for conservation agencies mandated with devising and implementing strategies to conserve populations at risk and prevent species extinctions. Prioritising management efforts and conservation interventions requires reliable information on species population trends, threats and vulnerabilities to environmental change, but unfortunately, such information is lacking for the majority of species (De Moor & Day, 2013; Ellender et al., 2017; Skelton, 2001; Tweddle et al., 2009), especially the recently identified taxa. This situation is not unique to South Africa, in that conservation strategies for freshwater fishes globally, particularly for species with little recognized economic value, are often hindered by the unavailability of literature on species' biology and population status (Moyle, Kiernan, Crane, & Quiñones, 2013). Thus, the need for an alternative method for estimating the vulnerability of freshwater species to climate change has been identified (Geist, 2011).

Moyle et al. (2013) developed a method that is repeatable and allows a rapid and systematic evaluation of freshwater fish vulnerability to anthropogenic stressors and climate change that draws upon expert opinion where empirical data are lacking. In addition to providing estimates of current (baseline) species vulnerabilities, the method captures information to estimate future vulnerability as a result of climate change. This is particularly important for Mediterranean climate regions where the effects of climate change on freshwater ecosystems are expected to be especially severe (Dallas & Rivers-Moore, 2014; Filipe, Lawrence, & Bonada, 2013; Moyle et al., 2013). For CFE fishes which now persist as highly fragmented

populations largely restricted to headwater habitats, these climate change-induced threats are likely to elevate the risk of extinction. In an attempt to provide an a priori assessment of the relative vulnerabilities of native CFE freshwater fishes to climate change and other human impacts, the vulnerability assessment method detailed in Moyle et al. (2013) was applied to provide a baseline of the risk status of the currently recognized species. As introduced non-native fishes are considered a major risk to native species in the region (Ellender & Weyl, 2014; Tweddle et al., 2009), the Moyle et al. (2013) assessment method was applied also to non-native fishes currently present in the CFE to understand better the interplay between climate change and the impacts of non-native species in the region.

## 2 | METHODS

The study area comprised the Cape Fold Ecoregion of South Africa. Freshwater fish species were those as detailed in Ellender et al. (2017), but do not include two *Pseudobarbus* species described subsequent to the assessments (Chakona & Skelton, 2017). Species names were corrected following Skelton (2016).

The method is a questionnaire based on expert opinion that employs 20 metrics, divided into two modules comprising 10 metrics each. Each module involves scoring a set of physiological, behavioural and ecological characteristics of a species to estimate its vulnerability in relation to climate change and other human impacts. Module 1 evaluates the 'baseline vulnerability' ( $V_b$ ) of a species to environmental change, which is the degree to which the species is declining independent of climate change (Table S1a, Supporting information), while module 2 focuses on the likely impact of climate change, 'climate change vulnerability' ( $V_c$ ) (Table S1b). Scores for each metric are summed to give a total score for each species in each module. Total scores fall within vulnerability rating categories ranging from 'Least Vulnerable' to 'Critically Vulnerable', with an additional category 'Likely to benefit' for Module 2 (Table S2). The full details of the vulnerability assessment method and metrics can be found in Moyle et al. (2013).

The level of certainty of the scores assigned to each metric is evaluated in two ways. First, each metric is assigned a 'best estimate' score based on published data and/or expert opinion, and an 'alternative' score which represents a less likely but still reasonable estimate for the given metric. Second, each score is assigned a certainty value of 'low', 'medium' or 'high' (Moyle et al., 2013; Table 1, Table S1a,b). No alternative score is assigned for situations where a high certainty was assigned to the best estimate. Local experts, identified by (and in some cases including) the authors, undertook vulnerability assessments for each native and non-native species of freshwater fish present in the CFE (see Table S3 for the list of assessors assigned to the different species, and Table S1a, b for the score sheets (developed by Moyle et al., 2013) that were completed by each assessor). Baseline and climate change vulnerability ratings, as well as associated levels of certainty, are presented for individual species, and for native and non-native species grouped together.

Spatial patterns of native fish vulnerability over the region were then visualized by projecting species vulnerability estimates onto

**TABLE 1** Baseline and climate change vulnerability ratings and certainty scores for native and non-native Cape Fold Ecoregion freshwater fish. Vulnerability rating interpretations are Vb1 or Vc1 = Critically Vulnerable, Vb2 or Vc2 = Highly Vulnerable, Vb3 or Vc3 = Less Vulnerable and Vb4 or Vc4 = Least Vulnerable. IUCN ratings are NE = Not Evaluated, DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered

Species name	Common name	Origin	Baseline vulnerability rating	Baseline certainty score	Climate change vulnerability rating	Climate change certainty score	IUCN rating
Native species							
<i>Austroglanis barnardi</i> <sup>a</sup>	Barnard's rock catfish	Native	V <sub>b3</sub>	Medium	V <sub>c2</sub>	Medium	EN
<i>Austroglanis gilli</i> <sup>a</sup>	Clanwilliam rock catfish	Native	V <sub>b3</sub>	High	V <sub>c2</sub>	Medium	VU
<i>Enteromius anoplus</i>	Chubbyhead barb	Native	V <sub>b3</sub>	Medium	V <sub>c2</sub>	Medium	LC
<i>Enteromius pallidus</i>	Goldie barb	Native	V <sub>b3</sub>	Low	V <sub>c2</sub>	Medium	LC
<i>Galaxias zebratus</i> <sup>a</sup>	Cape galaxias	Native	V <sub>b2</sub>	High	V <sub>c4</sub>	Medium	DD
<i>Labeo sebeeri</i> <sup>a</sup>	Clanwilliam sandfish	Native	V <sub>b2</sub>	High	V <sub>c1</sub>	Medium	CR
<i>Labeo umbratus</i>	Moggel	Native	V <sub>b4</sub>	Medium	V <sub>c4</sub>	Medium	LC
<i>Labeobarbus seeberi</i> <sup>a</sup>	Clanwilliam yellowfish	Native	V <sub>b2</sub>	Medium	V <sub>c1</sub>	Medium	VU
<i>Pseudobarbus afei</i> <sup>a</sup>	Eastern Cape redfin	Native	V <sub>b3</sub>	High	V <sub>c2</sub>	Low	EN
<i>Pseudobarbus burchelli</i> <sup>a</sup>	Breede River redfin	Native	V <sub>b2</sub>	High	V <sub>c3</sub>	High	EN
<i>Pseudobarbus burgii</i> <sup>a</sup>	Berg River redfin	Native	V <sub>b2</sub>	High	V <sub>c2</sub>	Medium	EN
<i>Pseudobarbus phlegethon</i> <sup>a</sup>	Fiery redfin	Native	V <sub>b3</sub>	High	V <sub>c2</sub>	Medium	EN
<i>Pseudobarbus skeltoni</i> <sup>a</sup>	Giant redfin	Native	V <sub>b2</sub>	High	V <sub>c1</sub>	High	NE
<i>Pseudobarbus tenuis</i> <sup>a</sup>	Slender redfin	Native	V <sub>b2</sub>	Low	V <sub>c2</sub>	Medium	NT
<i>Pseudobarbus verloreni</i> <sup>a</sup>	Verlorenvlei redfin	Native	V <sub>b2</sub>	High	V <sub>c2</sub>	Low	NE
<i>'Pseudobarbus' calidus</i> <sup>a</sup>	Clanwilliam redfin	Native	V <sub>b3</sub>	High	V <sub>c2</sub>	Medium	VU
<i>'Pseudobarbus' capensis</i> <sup>a</sup>	Berg-Breede River whitefish	Native	V <sub>b3</sub>	High	V <sub>c3</sub>	Low	EN
<i>'Pseudobarbus' erubescens</i> <sup>a</sup>	Twee River redfin	Native	V <sub>b2</sub>	High	V <sub>c3</sub>	High	CR
<i>'Pseudobarbus' serra</i> <sup>a</sup>	Clanwilliam sawfin	Native	V <sub>b2</sub>	Medium	V <sub>c1</sub>	Medium	EN
<i>Sandelia capensis</i> <sup>a</sup>	Cape kurper	Native	V <sub>b2</sub>	High	V <sub>c4</sub>	Medium	DD
Non-native species							
<i>Clarias gariepinus</i>	African sharptooth catfish	Non-Native	V <sub>b4</sub>	Medium	V <sub>c4</sub>	Medium	-
<i>Cyprinus carpio</i>	Common carp	Non-Native	V <sub>b4</sub>	Medium	V <sub>c4</sub>	High	-
<i>Gambusia affinis</i>	Western mosquitofish	Non-Native	V <sub>b4</sub>	Medium	V <sub>c4</sub>	Medium	-
<i>Labeo capensis</i>	Orange River mudfish	Non-Native	V <sub>b4</sub>	Medium	V <sub>c4</sub>	High	-
<i>Labeobarbus aeneus</i>	Smallmouth yellowfish	Non-Native	V <sub>b4</sub>	High	V <sub>c3</sub>	Medium	-
<i>Lepomis macrochirus</i>	Bluegill	Non-Native	V <sub>b4</sub>	Medium	V <sub>c3</sub>	Medium	-
<i>Micropterus dolomieu</i>	Smallmouth bass	Non-Native	V <sub>b4</sub>	Medium	V <sub>c3</sub>	High	-
<i>Micropterus floridanus</i>	Florida bass	Non-Native	V <sub>b4</sub>	Medium	V <sub>c3</sub>	High	-
<i>Micropterus punctulatus</i>	Spotted bass	Non-Native	V <sub>b4</sub>	Medium	V <sub>c3</sub>	Medium	-
<i>Micropterus salmoides</i>	Largemouth bass	Non-Native	V <sub>b4</sub>	Medium	V <sub>c3</sub>	Medium	-
<i>Oncorhynchus mykiss</i>	Rainbow trout	Non-Native	V <sub>b3</sub>	Medium	V <sub>c1</sub>	Medium	-
<i>Oreochromis aureus</i>	Israeli tilapia	Non-Native	V <sub>b4</sub>	High	V <sub>c4</sub>	Medium	-

(Continues)

TABLE 1 (Continued)

Species name	Common name	Origin	Baseline vulnerability rating	Baseline certainty score	Climate change vulnerability rating	Climate change certainty score	IUCN rating
<i>Oreochromis mossambicus</i>	Mozambique tilapia	Non-Native	V <sub>b</sub> 4	High	V <sub>c</sub> 4	Medium	-
<i>Pseudocrenilabrus philander</i>	Southern mouth-brooder	Non-Native	V <sub>b</sub> 4	High	V <sub>c</sub> 4	High	-
<i>Salmo trutta</i>	Brown trout	Non-Native	V <sub>b</sub> 2	Medium	V <sub>c</sub> 1	High	-
<i>Tilapia sparrmanii</i>	Banded tilapia	Non-Native	V <sub>b</sub> 4	High	V <sub>c</sub> 4	Medium	-
<i>Tinca tinca</i>	Tench	Non-Native	V <sub>b</sub> 4	Low	V <sub>c</sub> 4	High	-

<sup>a</sup>Endemic to the CFE

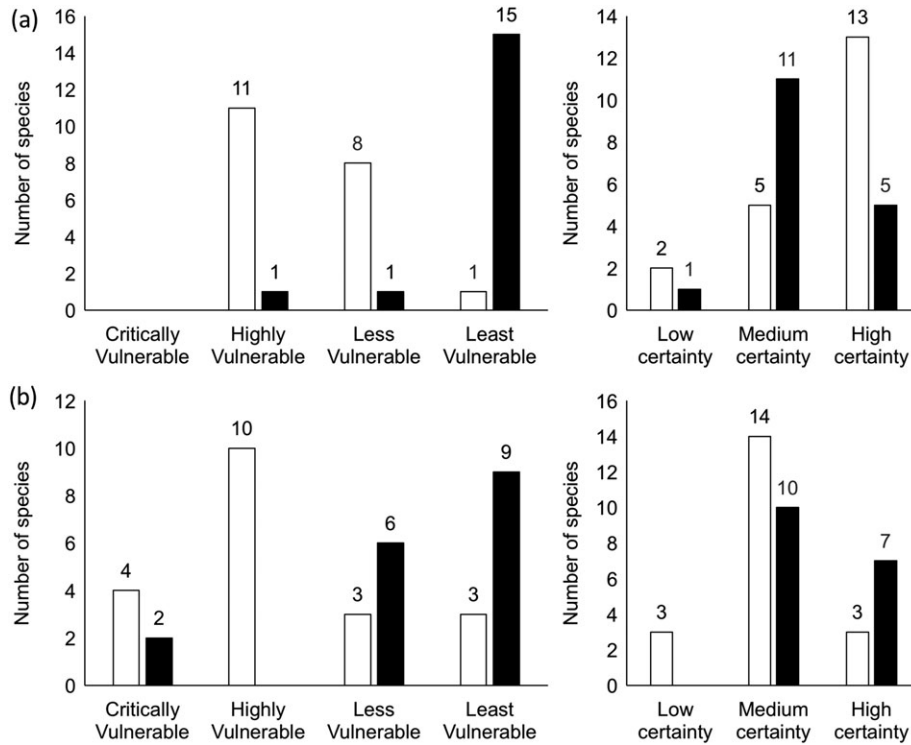
species distribution maps using ArcGIS® software, ArcMap 10.3 (ESRI, 2011). Separate vulnerability projections were developed for baseline and climate change vulnerabilities, and for each, both 'all' and 'high' certainty data are presented. The species distribution data represent species records post-2000 compiled by the authors from all available sources of reputable CFE fish distribution information including scientific publications, published reports and institutional databases (including those of CapeNature, the South African Institute for Aquatic Biodiversity and South African National Parks).

### 3 | RESULTS

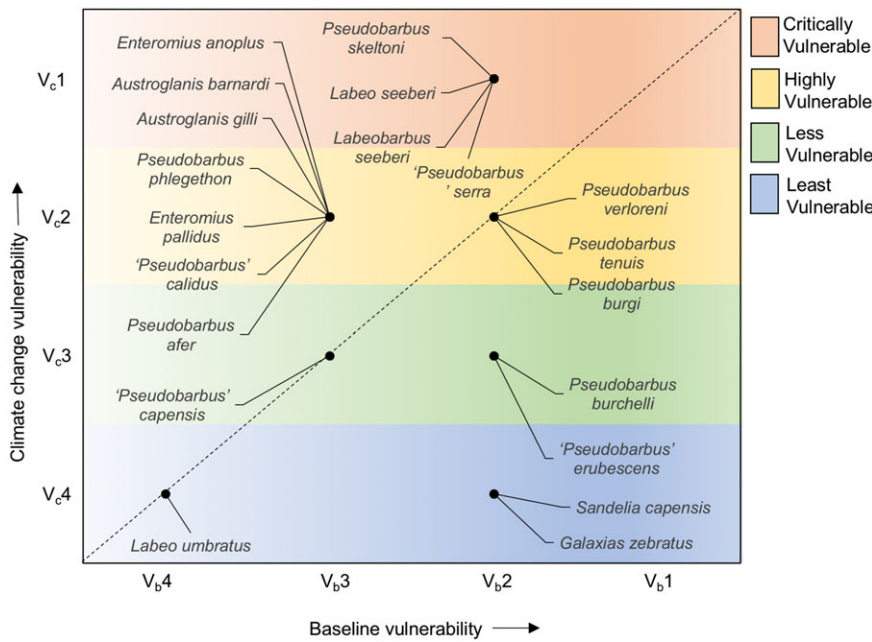
Vulnerability assessments were conducted by reviewers for 20 native and 17 non-native freshwater fishes present in the CFE (Table 1; Table S3). Native species generally had higher baseline vulnerabilities than non-native species (Figure 1a, Table 1). The majority of native species fell within the Highly Vulnerable (11 species) and Less Vulnerable (8 species) categories, while the majority of non-native fishes (15 species) were assessed as Less Vulnerable. Native species in the Highly Vulnerable category included the cyprinids '*Pseudobarbus*' *erubescens*, '*Pseudobarbus*' *serra*, *Pseudobarbus burchelli*, *Pseudobarbus burgi*, *Pseudobarbus skeltoni*, *Pseudobarbus tenuis*, *Pseudobarbus verloreini*, *Labeo seeberi* and *Labeobarbus seeberi*, the anabantid *Sandelia capensis* and the galaxiid *Galaxias zebratus*. No species were classified as Critically Vulnerable in the baseline module. Certainty scores were high for the majority of native species (14 species had high certainty, five had medium certainty), while most of the non-native species had medium certainty (11 species had medium certainty, five had high certainty) (Figure 1a, Table 1).

However, for the climate change module, four native species were classified as Critically Vulnerable, and of the remaining native species, the majority (10 species) fell within the Highly Vulnerable category, with three species in each of the Less and Least Vulnerable categories (Figure 1b). Eleven of the 20 native species were classified as being more vulnerable in the climate change module than in the baseline module, five species had the same baseline and climate change vulnerabilities, and the remaining four species had lower climate change vulnerabilities than baseline vulnerabilities (Figure 2). Of the species expected to become more vulnerable with climate change, *P. serra*, *Labeo seeberi*, *Labeobarbus seeberi* and *P. skeltoni* shifted from Highly Vulnerable to Critically Vulnerable; and *Enteromius anoplus*, *Austroglanis barnardi*, *Austroglanis gilli*, *Pseudobarbus phlegethon*, *Pseudobarbus afer*, *Enteromius pallidus* and '*Pseudobarbus*' *calidus* shifted from Less Vulnerable to Highly Vulnerable (Figure 2). Most non-native species fell within the Less Vulnerable (six species) and Least Vulnerable (nine species) categories. No non-natives were classed as Highly Vulnerable, but both salmonids *Oncorhynchus mykiss* and *Salmo trutta*, which require cool well oxygenated waters, were classified as Critically Vulnerable (Figure 1b).

The baseline vulnerability map for all certainties shows that records of Highly Vulnerable species are spread throughout the region, but are somewhat more concentrated in the south-west CFE (Olifants-Doring, Berg, Breede, Gouritz and coastal catchments; Figure 3a). In



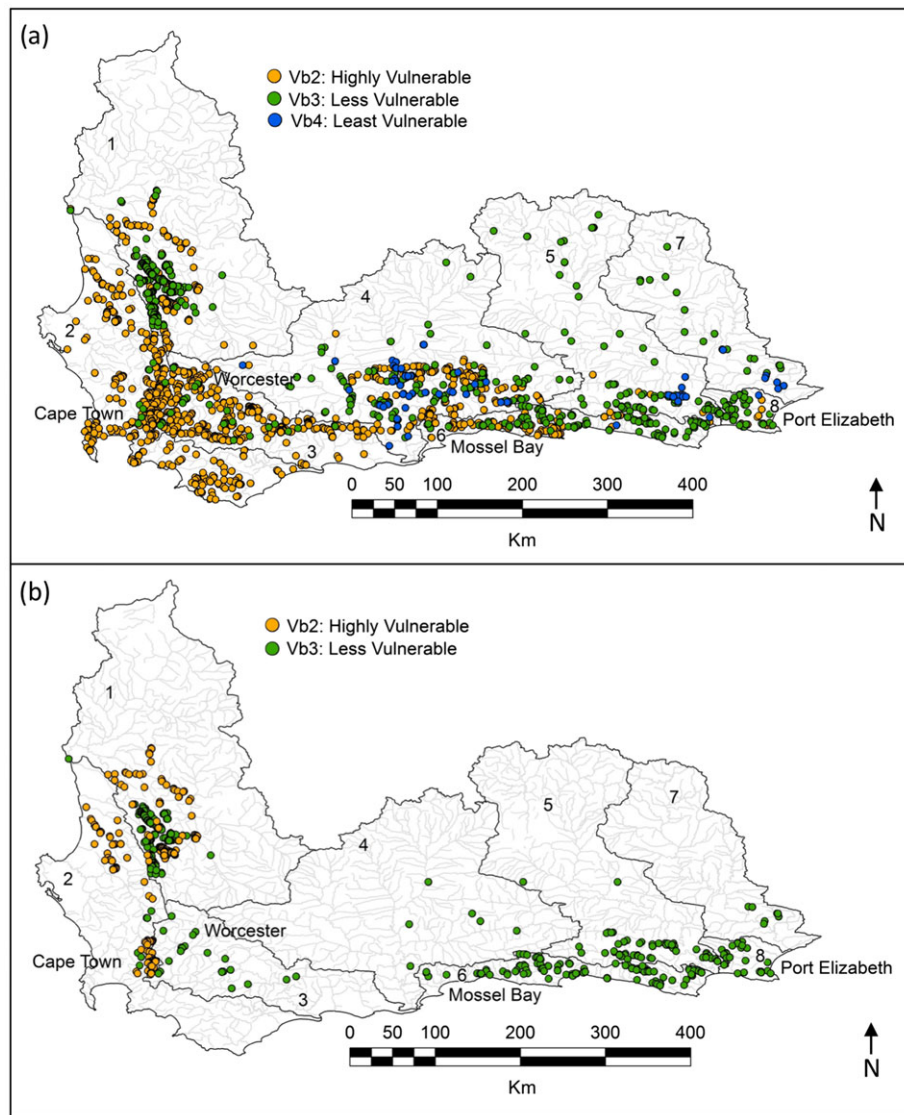
**FIGURE 1** Baseline (a) and climate change (b) vulnerability ratings and certainty scores for native (white bars) and non-native (black bars) Cape Fold Ecoregion freshwater fish. Numbers above bars indicate the total number of species within a category



**FIGURE 2** Baseline and climate change vulnerabilities of native Cape Fold Ecoregion freshwater fishes. Coloured bands represent climate change vulnerabilities (y-axis), and the opacity of the bands indicates increasing baseline vulnerability (x-axis). Species falling above the dotted line had higher climate change than baseline vulnerabilities, species below the line had lower climate change than baseline vulnerabilities, and species on the line had the same baseline and climate change vulnerabilities

contrast, records for Less and Least Vulnerable species were somewhat more common in the eastern half of the region than in the west. The high certainty baseline map comprises far fewer species distribution records, reflecting the relatively low certainty associated with assessments for several species (Table 1). For the high certainty analysis, the distributions of Highly Vulnerable species are largely confined to rivers in the Olifants-Doring and upper Berg and Breede catchments.

The climate change vulnerability map for all certainties shows that species classified as Highly Vulnerable are distributed throughout the region, while Critically Vulnerable species are concentrated in the south west, specifically in the Olifants-Doring catchment and upper Berg and Breede river catchments (Table 1; Figure 4). The high certainty map also shows a concentration of Highly and Critically Vulnerable species in rivers in the Olifants-Doring, upper Berg and upper Breede catchments, and a concentration of Highly (but



**FIGURE 3** Baseline vulnerability projections for native freshwater fishes in Cape Fold Ecoregion based on (a) all species and (b) species with high certainty scores only (see Table 1 for species-level certainty scores). Species distribution data represent species records post-2000 compiled by the authors from all available sources as part of Water Research Commission-funded project WRC K5/2337. The smallscale redbfin *Pseudobarbus asper* and the Tradouw lineage of *Pseudobarbus burchelli* (Burchell's redbfin) were not included in the assessment. Catchments are: 1 = Olifants-Doring, 2 = Berg, 3 = Breede, 4 = Gouritz, 5 = Gamtoos, 6 = coastal, 7 = Sundays and 8 = Swartkops

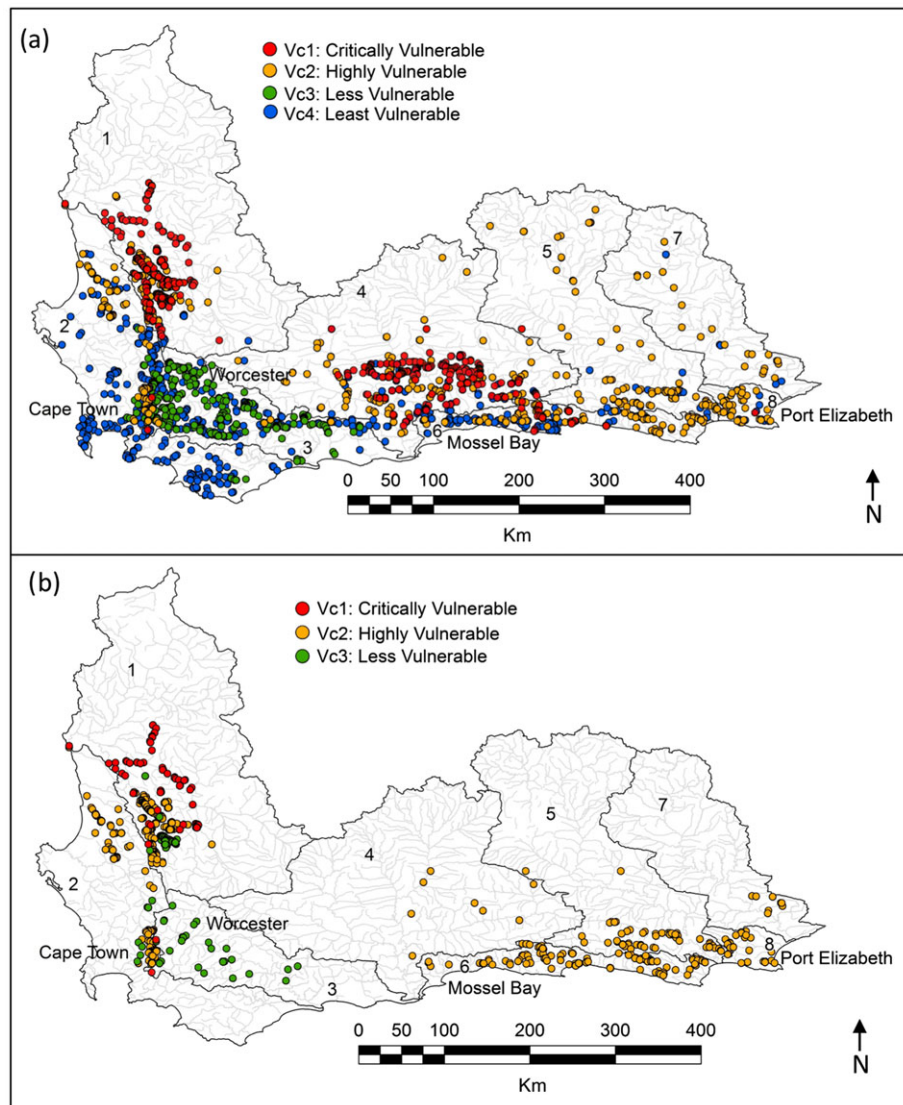
not Critically) Vulnerable species in the eastern half of the region including the coastal catchments between Mossel Bay and Port Elizabeth.

#### 4 | DISCUSSION

In South Africa, the limited availability of resources for conservation efforts, especially for aquatic ecosystems, underpins the need to identify management priorities in order to prevent species extinctions (Impson, 2016). Biodiversity managers, therefore, need reliable information concerning the vulnerability of different native species to a variety of global change processes so that proactive conservation measures can be developed and populations prioritized. Data on biology and population trends, which typically underpin vulnerability assessments, are inadequate or unavailable for many of these species

(see review in Ellender et al., 2017) making it difficult to identify conservation priorities and focus limited management resources (De Moor & Day, 2013; Skelton, 2001; Tweddle et al., 2009). Employing the vulnerability assessment method of Moyle et al. (2013) enabled the present study to capitalize on available expert knowledge to supplement existing data and thereby produce relatively well-informed estimates of present and future native and non-native species vulnerabilities.

The baseline vulnerability estimates presented here are broadly consistent with available literature on native fish vulnerabilities in the CFE (Tweddle et al., 2009; Weyl et al., 2014) and medium to high confidence levels of assessors are due to the completion of recent surveys across much of the CFE. Key factors responsible for high vulnerabilities include competition with, and predation by, non-native species and a range of human induced impacts including habitat alterations, pollution and water abstraction that have led to the degradation or loss of



**FIGURE 4** Climate change vulnerability projections for native freshwater fishes in Cape Fold Ecoregion based on (a) all species and (b) species with high certainty scores only (see Table 1 for species-level certainty scores). Species distribution data represent species records post-2000 compiled by the authors from all available sources as part of Water Research Commission-funded project WRC K5/2337. The smallscale redbfin *Pseudobarbus asper* and the Tradouw lineage of *Pseudobarbus burchelli* (Burchell's redbfin) were not included in the assessment. Catchments are: 1 = Olifants-Doring, 2 = Berg, 3 = Breede, 4 = Gouritz, 5 = Gamtoos, 6 = coastal, 7 = Sundays and 8 = Swartkops

aquatic habitats (Clark et al., 2009; Skelton, 2001; Tweddle et al., 2009). More than half (55%) of the native species assessed here were classified as Highly Vulnerable, which corresponds closely with the proportion of threatened (Vulnerable, Endangered or Critically Endangered) species (57%) in the IUCN Red List. There are, however, also some noteworthy differences between the results of the present assessment and the current IUCN listings. For example, in the present assessment *P. capensis* (formerly *Barbus andrewi*) is classified as Less Vulnerable based on its present population size, trends and susceptibilities to current environmental stressors. This species was evaluated as Endangered in the 2007 IUCN Red List based on the small area of occupancy and highly fragmented populations. The discrepancy between the two assessment methods demonstrates the applicability of each tool in a conservation context. The Red List focuses on the conservation status while the Moyle et al. (2013) assessment allows for categorizing risk to different species and for contrasting risk among

species. Another discrepancy between the two approaches is reflected by the evaluation of *P. tenuis* as Highly Vulnerable in the present study, but as Near Threatened in the 2007 IUCN Red List. It is interesting that no species were identified as Critically Vulnerable in the present baseline vulnerability assessments.

That non-native species had lower baseline vulnerabilities than native species is not surprising. Many of the established non-native fishes (e.g. *Micropterus salmoides*, *Lepomis macrochirus*, *Cyprinus carpio*, *Gambusia affinis*, *Clarias gariepinus*), can tolerate a relatively wide range of environmental conditions and are generally less sensitive to decreases in water and/or habitat quality than most of the native species (Ellender & Weyl, 2014; Skelton, 2001). Moreover, the distributions of some of these species are expanding because of active introductions into new habitats, or because they lack natural population controls outside of their native ranges (Ellender & Weyl, 2014; Shelton, Samways, & Day, 2015; Weyl, Daga, Ellender, & Vitule,

2016; Weyl, Ellender, Wasserman, & Woodford, 2015). However, the salmonids *O. mykiss* and *S. trutta* tolerate a relatively narrow range of environmental conditions, and are highly sensitive to habitat degradation (Ebersole, Liss, & Frissell, 2001; Ellender, Rivers-Moore, Coppinger, Bellingan, & Weyl, 2016; Leprieur et al., 2006), hence their relatively high vulnerabilities.

Results for the climate change vulnerability assessments indicate that vulnerability levels are expected to increase for both native and non-native species when climate change-related factors are taken into consideration. Importantly, the cyprinids *P. serra*, *Labeo seeberi*, *Labeobarbus seeberi* and *P. skeltoni* shift from Highly Vulnerable to Critically Vulnerable. The factors responsible for these shifts differ from species to species. In the case of *P. skeltoni*, its distribution has become so restricted that any intensification of current threats, particularly non-native species impacts or marked changes in habitat conditions, could have severe adverse consequences for remaining populations (Chakona & Swartz, 2013; Kadye, Chakona, & Jordaan, 2016). However, the larger-bodied cyprinids *P. serra*, and *Labeobarbus seeberi* have wider distribution ranges and greater population sizes, but are acutely dependent on seasonal temperature cues and flow conditions for spawning (Paxton & King, 2009). With temperatures expected to increase, and high flow events expected to become more extreme and erratic (Dallas, 2013; Dallas & Rivers-Moore, 2014), the frequency of successful spawning events is likely to decrease either because of inadequate flow conditions, or mismatched temperature and flow cues.

*Labeo seeberi*, like *P. skeltoni*, has a very restricted distribution, and recruitment in remaining habitats is severely compromised by the presence of non-native fishes and excessive degradation of aquatic habitats. It appears to undergo spawning migrations into seasonal tributaries and has a very restricted spawning period associated with specific thermal and flow spawning conditions which could well be affected by projected changes in rainfall and temperature. *Labeo seeberi* is among the CFE's most threatened freshwater fish owing to its preference for mainstem river reaches where non-native fish species predominate, rather than tributaries. A Biodiversity Management Plan for Species (BMP-S) drafted in 2014 provides guidance for the future management of this species (DEA, 2014). Evidence gathered during the development of the BMP-S led to the IUCN threat status for the species being adjusted from Endangered to Critically Endangered as a result of a much narrower than expected present-day distribution and paucity of breeding sites free of non-native species.

While the consequences of climate change for non-native species are generally expected to be less severe, the range of occupancy of the salmonids *O. mykiss* and *S. trutta* is likely to contract under current climate change scenarios. As water temperatures and rainfall variability increase, trout distributions may contract into cooler, higher-altitude river reaches that are accessible. This was demonstrated by Ellender et al. (2016) for *S. trutta* and *O. mykiss* in the Keiskamma River system, South Africa, and has also been forecast in their native and introduced ranges in the USA (Bryant, 2009; Ebersole et al., 2001; Flebbe, Roghair, & Bruggink, 2006). The remaining 15 non-native species are considered warm-water fishes and are therefore probably more resistant to impacts of climate change, and their distributions and

abundances are unlikely to decrease unless actively controlled through management interventions.

Results here, matched closely by the IUCN listings, indicate that levels of vulnerability (both baseline and climate change perspectives) are highest in the Olifants-Doring, Berg, Breede, Gouritz and coastal catchments. Thus, the south-western section of the CFE should be a priority area for freshwater fish conservation efforts, but it is noted that highly vulnerable species occur throughout the Ecoregion (Figure 4). The Cedarberg Mountains in the Olifants-Doring catchment and the upper Berg and Breede River catchments can be considered freshwater fish 'vulnerability hotspots' in the CFE – the most critical areas from a conservation standpoint, and areas where limited conservation resources (Impson, 2016) and active management should be given priority. Active management approaches for conserving native fish populations should include non-native fish eradication efforts (such as those described in Weyl et al., 2014 and Shelton et al., 2017) where non-native species directly threaten native species, as well as efforts to rehabilitate degraded aquatic habitats. Furthermore, it is imperative to ensure that these vulnerability hotspots are incorporated into areas formally demarcated for conservation, such as South Africa's Freshwater Ecosystem Priority Areas (FEPAs, Nel et al., 2011) and CapeNature's formal Protected Area Expansion Strategy.

The clear difference in the number of data points between the all certainty and high certainty projections (Figure 1; Figure 4) emphasizes that confidence was not high for several of the species assessed (Figure 3), and the results for medium and low certainty species should be interpreted with caution. In particular, certain areas such as the Gouritz catchment, and some of the adjacent coastal systems, contained high-risk species, but certainties around future vulnerabilities were low. Such areas should be given priority with more intensive research on species distributions and vulnerabilities. Involving multiple assessors per species would improve confidence in the vulnerability classifications and should be considered for future studies (Moyle et al., 2013). This is particularly pertinent for the climate change module, where only three of the 20 species were assessed with a high certainty. An important additional consideration is that the taxonomy of many CFE fish taxa are subject to continuing revision (Ellender et al., 2017). For example, *P. afer* has been divided into four species following a recent review of this complex (Chakona & Skelton, 2017). Periodic re-evaluation of vulnerability scores is therefore necessary following description of new species and improved understanding of species distributions. These results highlight the vulnerability of CFE fishes to global change processes while emphasizing the need for further studies on the biology, distribution and population trends for CFE freshwater fishes, particularly the native species that were assigned low certainty.

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#### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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