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Application of a trait-based climate change vulnerability assessment to determine management priorities at protected area scale

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Abstract

Estimating and planning for the impacts of climate change on the biodiversity of protected areas is a major challenge for conservation managers. When these areas are topographically heterogenous and contain species' entire ranges, this challenge is exacerbated because the coarse spatial scales of Global Circulation Model projections provide limited information for within-park management. South Africa's Table Mountain National Park, home to three endemic amphibian species in just ~24,500 hectares, provides a case study for identifying conservation needs under climate change. Selecting the park's herpetofauna as pilot taxa, we identified life history and demographic characteristics believed to make species more sensitive and less able to adapt to climate change. We organized these into assessment frameworks and, through a combination of literature review and expert elicitation, reviewed and used them to assess climate change vulnerability of 18 amphibian and 41 reptile species. The assessment highlighted that 73% and 67% of the park's reptile and amphibian species, respectively, had at least one high-sensitivity and low-adaptive capacity trait. Using ordinal and additive scoring methods, we identified the species most vulnerable to climate change and highlight the park areas containing their highest concentrations. These areas will be used to inform landscape-scale management priorities and park use zones. The current IUCN Red List assessments for these species do not incorporate climate change vulnerability. Considering some species appear to be threatened by climate change, their conservation needs might be underestimated. Identifying the most vulnerable species and the mechanisms underpinning their vulnerability can guide the identification and prioritization of conservation needs, while the highlighted knowledge gaps inform priorities for monitoring and research. While comprehensive climate change adaptation planning for Table Mountain National Park requires additional assessment of other taxonomic groups, this trait-based assessment example highlights a viable tool for assessing climate change vulnerability in protected areas.

KEYWORDS

adaptive capacity, adaptive management, climate change vulnerability assessment, herpetofauna, IUCN Red List, life history, management intervention, resilience

1 | INTRODUCTION

The impacts of climate change on global biodiversity are expected to intensify over the coming decades. Climate change vulnerability assessments (CCVAs) attempt to predict the degree to which climate change will impact particular species, subspecies, or populations (Foden & Young, 2016), and are therefore valuable tools for informing adaptive management. However, accurately estimating these impacts and identifying where they will be felt most strongly remains a major challenge for the scientific community, particularly at the scale of an individual protected area (PA) (Foden & Young, 2016).

Climate change is altering the effectiveness of static PAs in conserving many of the species historically occurring there, and the magnitude and degree of threat conferred by these changes on such species are largely unquantified (Elsen et al., 2020; Hannah, 2008). Conservation managers need guidance for making decisions around PA planning, expansion, rehabilitation, ex situ conservation and assisted migration (Prober et al., 2019). Climate change is often cited as a major threat to the biodiversity of PAs, yet actual consideration of sensitivity and adaptive capacity of flora and fauna to climate change is infrequently considered in planning, particularly in the short term. However, without consideration of individual species' climate change vulnerabilities, conservation managers are left with a potentially significant blind spot. For example, outputs of Vulnerability assessments can help identify which species and areas are priorities for monitoring following extreme events (e.g., fires, temperature anomalies, storms, floods and drought). This can aid understanding of species' responses to such events and the degree to which intervention may or may not be required (Ameca y Juárez EI et al., 2013; Measey et al., 2021).

Table Mountain National Park (hereafter TMNP) is a small PA (~24,500 hectares) located in the extreme southwest of the hyper-diverse Cape Floristic Region of South Africa. By 2050, average annual air temperature within the city of Cape Town Municipality is predicted to have risen by 1.2–1.9°C (under RCP 4.5 where global anthropogenic CO_2 emissions peak by 2040; Le Roux et al., 2019). However, trends already documented suggest that such estimates may be conservative, as the park experienced an average air temperature rise of 1.05°C (minimum temperature) and 1.25°C (maximum temperature) between 1960 and 2010 (van Wilgen et al., 2016). The park's location on a southerly peninsula surrounded by a combination of sea and dense urban settlement, together with its high biodiversity and large number of threatened species, make understanding patterns of species climate change vulnerability essential for effective management.

Currently, there are three commonly used approaches for carrying out CCVAs: correlative, mechanistic and trait-based (Foden et al., 2018). Each has its own data, time and accuracy constraints. The correlative or "climate-matching" approach uses the observed geographical distribution of a species to estimate the current climatic conditions in which the species occurs (i.e., its approximate realized niche or "climate envelope"). Climate envelopes are then combined with climate projections to model the distribution of suitable climatic space in the future (Foden et al., 2018; Pacifici et al., 2015). Species' vulnerability can be predicted by examining the difference between the location, size and fragmentation of its current and projected future climatic space (Foden et al., 2018; Garcia et al., 2014; Huntley et al., 2007). However, confidence in correlative models is reduced by uncertainties surrounding the relationship between the realized climate niche and underlying climatic tolerance limits of the organism, and by uncertainty around current climate change projections (Rowland et al., 2011). The latter is particularly acute at the scale of small PAs because the general circulation models used to predict future climate conditions do so at scales coarser than the biological and environmental data used to train correlative models. This is problematic for species that have few known locality points (typically rare or under-sampled species) or have small geographic distributions (Foden et al., 2018; Guisan & Thuiller, 2005; Pacifici et al., 2015).

Mechanistic models use process-based simulations incorporating known biological tolerances, interactions and processes to predict species' climate change responses (Foden & Young, 2016; Morin & Thuiller, 2009). Mechanistic models can be categorized into niche or demographic models (Foden et al., 2018). Demographic models assess the species' probability of extinction. Alternatively, niche models predict the potential distribution of species by estimating their fundamental niche, defined through measurements of the species' physiological tolerances (e.g., Monahan, 2009; Sunday et al., 2012), and through energy balance equations (e.g., Kearney & Porter, 2009). The typical requirements for expertise and experience, extensive and detailed data, and significant funding limit the viability of mechanistic models for rapid and multispecies assessments (Foden et al., 2018; Foden & Young, 2016; Kearney & Porter, 2009; Pacifici et al., 2015).

A trait-based vulnerability assessment uses knowledge of associations between species' biological and life history traits and expected climate change stressors to quantify, categorize and/or rank species' vulnerability, allowing for the simultaneous examination of climate change stressors and species-specific responses to these (Foden & Young, 2016). A trait-based assessment uses a "framework" of life history traits encompassing each species' sensitivity, adaptive capacity and exposure to climate change. The approach can become limited by large gaps in understanding of species' life histories and the complexities around defining thresholds of risk for traits quantified by continuous data. However, trait-based assessments are applicable to small-ranged and under-sampled species, while also being the least time-intensive and cheapest approach, increasing their practicality for conservation practitioners (Foden et al., 2018; Foden & Young, 2016). The outputs of the assessment can be combined with species distribution data to determine where and why species are vulnerable, aiding conservation planning and intervention (Foden et al., 2013; Nyboer et al., 2021). Such assessments have been used globally (Böhm et al., 2016; Foden et al., 2013; Hossain et al., 2019; Kopf et al., 2017; Zhang et al., 2019) and regionally (Cabrelli et al., 2014; Case et al., 2015; Chin et al., 2010; Gardali et al., 2012; Hare et al., 2016; Jamwal et al., 2021; Meng et al., 2016; Mims et al., 2018; Nyboer et al., 2019; Nyboer et al., 2021; Tingley et al., 2013; Triviño et al., 2013) for a variety of taxa including birds, reptiles, amphibians, corals, primates and fish, among others. Despite being well suited to application in PAs, trait-based vulnerability assessments to our knowledge have yet to be applied to inform priorities at the scale of a single PA.

We selected a trait-based CCVA for TMNP because the presence of four narrowly distributed amphibian species within the study area, coupled with the area's small geographic extent and highly varied topography, greatly reduce the applicability of distribution modeling to its species (Foden & Young, 2016; Platts et al., 2014). We elected to pilot the approach on reptiles and amphibians because their body temperatures are a function of environmental temperature, making them sensitive to changing climate and therefore good indicators of its impacts.

TMNP and its immediate surrounding areas are home to 18 amphibian species (four endemic or near-endemic to the park [within the park, and up to 10 km from its boundary]), and 41 species of reptiles. Three amphibian species are listed as Critically Endangered on the IUCN Red List, of which two are endemic to TMNP (IUCN, 2019). Movement, reproduction, metabolism and development of ectotherms are all influenced by local temperature shifts (Angilletta, 2009; Huey et al., 2012; Sinclair et al., 2016). Optimal performance of these species can be maintained by regulating body temperature (Kearney & Porter, 2009), or by plastic or evolutionary responses in the longer term (Huey et al., 2012). However, where activity is strongly coupled to temperature, species may face shrinking windows of opportunity as temperatures rise, reducing the time during which thermal conditions allow for activity, affecting optimal performance or fitness (Sinervo et al., 2010).

Here we: i) identify the relative climate change vulnerability of 18 amphibians and 41 reptiles; ii) identify areas of high concentrations of climate change vulnerable species to inform spatial management and protection of vulnerable species; iii) examine limitations of data availability and quality. We discuss the benefits and caveats of using the trait-based vulnerability assessment approach at this scale. The climate vulnerability "lens" proposed here aims to provide managers with a more complete picture of threats to the species they conserve, a way to identify novel priorities, and a quantitative foundation to direct proactive management intervention.

2 | METHODS

Lists of reptile and amphibian species known to occur in TMNP were compiled based on the IUCN Red List species distribution data (IUCN, 2013, 2016, 2018) and expert herpetological knowledge of the park. To adequately represent the local diversity, we also included the southern adder (*Bitis armata*), a species of conservation concern (Vulnerable; Maritz & Turner, 2018), which has not been recorded within the park but might have historically occurred in some lowland areas near or within the park. The final list comprised of a total of 41 reptile and 18 amphibian species (Supporting Information, hereafter S1).

2.1 | Development of the scoring framework

For the trait-based assessment, reptile- and amphibian-specific sensitivity (e.g., reliance on an environmental cue) and adaptive capacity (e.g., dispersal ability) trait

TABLE 1 Traits used to score reptile species' vulnerability, the variables and vulnerability thresholds used to score each trait, and n, the number of species classified as high, low and unknown for each trait and threshold

Sensitivity					
Trait set[a]	Traits	Weighting[b]	Variable to score	Vulnerability threshold	*n*
A	RS1: Habitat specialization	Medium	Number of substrate types present in species range (Batjes 2004)	High = Species occurs on only one substrate type	0
				Low = Species on >1 substrate type	41
A	RS2: Microhabitat specialization	High	Microhabitat types used by the species (Fossorial, Saxicolous, Arboreal, Terrestrial, Under dead organic matter, Semi-aquatic, Termite mounds)	High = Species is reliant on dead organic matter as a microhabitat	0
				Low = Species relies on microhabitats unlikely to be affected by climate change	41
A	RS3: High elevation specialistc	Low	Minimum elevation at which the species occurs	High = Species is found only within top 20% of highest mountain peak	0
				Low = Species occurs at a range of elevations	41
B	RS4: Narrow temperature tolerance[c]	High	Average absolute deviation in temperature across the species' historical range (Fick & Hijmans 2017)	High = Lowest 25% (value)	11
				Low = Highest 75% (value)	30
B	RS5: Narrow precipitation tolerance[c]	High	Average absolute deviation in precipitation across the species' historical range	High = Lowest 25% (value)	11
				Low = Highest 75% (value)	30
B	RS6: Intolerant of changes to fire regime	High	Evidence of fire-based mortality and/or fire listed as a threat in the IUCN Red List	High = Evidence of fire-based mortality and/or listed as a threat on the IUCN Red List	6
				Low = Affected by lack of fire or associated with habitat less affected by fire e.g., semi-aquatic	16
				Unknown = Relationship uncertain	19
B	RS7: Seasonal activity period restricted by temperature/rainfall	Medium	Evidence of seasonal inactivity because of high temperatures or low precipitation	High = Evidence of seasonal inactivity related to climatic conditions	2
				Low = Species is active year-round	39
B	RS8: Sensitive to decline in cloud/fog cover	High	Evidence of the species' reliance on cloud cover/fog to remain within its environmental tolerances	High = Published evidence or expert expectation	8
				Low = Species activity not limited by presence of cloud cover or fog	32
				Unknown = No understanding	1
B	RS9: Low environmental heterogeneity within range[c]	Medium	Mean score of vector ruggedness measure (Sappington et al. 2007)	High = Highest 25% (value)	11
				Low = Highest 75% (value)	30
D	RS10: Narrow diet breadth	Low	Evidence of species having high dietary specialization (morphologically and/or physiologically determined)	High = Species relies on one species for the majority (>90%) of its food resources	0
				Low = Species consumes a wide variety of food types	41
E	RS11: Endemic/rare	High	Endemic to Table Mountain	High = Species is endemic or near-endemic (within 10 km) to TMNP	0

TABLE 1 (Continued)

Sensitivity					
Trait set[a]	Traits	Weighting[b]	Variable to score	Vulnerability threshold	*n*
			National Park (TMNP), Cape Floristic Region (CFR), South Africa (South Africa), southern Africa, Africa or multiple continents	Low = Endemic to CFR, SA, southern Africa, Africa or multiple continents	
F	RS12: Semelparous?	Low	Evidence that the species has a single reproductive episode before death.	High = Evidence present	0
				Low = Evidence absent	31
				Unknown = Uncertain	0
F	RS13: Limited to a single annual reproductive event	High	1. Maximum number of clutches per year	High = Reproduce ≤1 per year and timing limited to specific periods.	22
			2. Ability to reproduce at any time of year	Low = Can breed >1 per year at anytime	12
				Unknown = Uncertain	7
Low Adaptive Capacity					
G	RL1: Dispersal limited by physical barriers	High	Location of species' distribution relative to Cape Agulhas (Africa's southern tip)	High = The species' entire distribution is within 10 latitudinal degrees to the most southerly point of Africa	0
				Low = Species distribution covers >10 degrees of latitude	41
H	RL2: No commensalism with humans	High	Evidence of ability to use human dominated landscapes	High = Species is sensitive to anthropogenic modification of its environment	31
				Low = Evidence that the species is able to move through and use human dominated landscapes	10
G & H	RL3: Foraging mode limits behavior adaptation	High	Foraging behavior of the species	High = Diurnal active visual forager	9
				Low = Alternative foraging behavior	30
				Unknown = Uncertain	2
I	RL4: Low microevolutionary potential	High	a. Mean annual reproductive output	High = ≤2 offspring per year (a). Evidence of low genetic diversity within populations, and/or highly fragmented populations (b)	11
			b. Genetic diversity and degree of population fragmentation	Low = Evidence contradictory to that of high threshold	30

[a]Trait set: A. Specialized habitat and/or microhabitat requirements; B. Narrow environmental tolerances or thresholds that are likely to be exceeded due to climate change at any stage in the life cycle; C. Dependence on a specific environmental trigger or cue that is likely to be disrupted by climate change; D. Dependence on interspecific interactions which are likely to be disrupted by climate change; E. Rarity; F. Sensitive life history; G. Poor dispersal ability; H. Limited behavioral adaptation; I. Poor evolvability.

[b]Expert weighting refers to the degree of relative importance a trait has on the sensitivity or adaptive capacity of a species when considered independently from the other traits.

[c]Allocated arbitrary thresholds due to the absence of empirical data for biologically meaningful thresholds.

frameworks were created following Foden and Young (2016) and Foden et al. (2018). The frameworks were based on traits or characteristics used previously in global assessments of these taxa (Böhm et al., 2016; Carr, 2011; Foden et al., 2013), tailored through an extensive literature review of the life histories and associated climate change vulnerabilities of each species (S2a contains hypotheses and methods for each trait included in the two frameworks). Draft frameworks were refined separately for reptiles and amphibians by taxon experts during an expert workshop with the final frameworks including 13 traits thought to affect sensitivity (e.g., being a habitat specialist) and four traits thought to affect adaptive capacity (e.g., not being able to move through modified landscapes, Tables 1 and 2). A method for scoring each trait was decided, for example temperature tolerances were determined by calculating the average absolute deviation (Fick & Hijmans 2017) in temperature across the species' range (details in Tables 1, 2 and S2). Thresholds set for each trait enabled categorization into the vulnerability categories: "Low", "High" or "Unknown" (see Foden et al., 2013).

2.2 | Sensitivity and adaptive capacity traits and scoring

We collected trait data for each species using literature and the IUCN Red List (IUCN, 2019), as well as expert opinion where necessary. Where a species had traits for which no published literature or sufficient expert knowledge were found, it was scored as 'Unknown'. Certain traits required distribution data (e.g., Narrow temperature/precipitation tolerances [RS4-5; AS4-5], or Dispersal limited by physical barriers [RL1; AL1]; see S1 2a). While our primary interest was to prioritize species that occur within the park, some species have a greater proportion of their total distribution outside of the park. Vulnerability was therefore assessed across species' entire distributions, for example, calculating temperatures experienced across their entire range as indicative of niche breadth as opposed to only using a species' park range. For this, global distribution polygons from IUCN Red List spatial data and mapping resources (IUCN, 2019) were used, and further refinements were made by local experts to include the most up-to-date understanding of local distribution. Detailed information on hypotheses, methods, uncertainties and data sources for each trait and species are provided in S2, S4, S5 and S6.

To combine trait scores, we used a combination of ordinal and additive scoring methods. Climate models for the study area were only available at coarse resolutions that provided little insight into the topographic variability and microclimates (J. Slingsby pers. comm.), making it appropriate to assess only sensitivity and adaptive capacity in this study, and not spatial exposure. For assigning ordinal scores, we set thresholds to define ordinal high and low scores for each trait (Böhm et al., 2016; Foden et al., 2013). The presence of one or more high scores within either the sensitivity or adaptive capacity dimension led to a high score being given for that particular dimension. Species with high sensitivity and low adaptive capacity were scored the most vulnerable to climate change. Once the presence or absence of both high sensitivity and low adaptive capacity traits had been determined, we re-scored each species using an additive method adapted from Graham et al. (2011) and Zhang et al. (2019). We calculated an overall vulnerability score for each species by applying the following formula:

$$\text{Vulnerability} = (S1 + S2 + \dots Sn)/N.$$

where S1, S2,...Sn are scores assigned to traits 1 to n and N is the number of traits used with data present for a particular species (for working example, see S2b). Not all sensitivity and adaptive capacity traits will have an equal impact on a species' vulnerability to climate change. To address this, we weighted traits with values of 1 (Low), 2 (Medium), or 3 (High) according to experts' understanding of their importance to the assessed species group (Tables 1 and 2). Additive scores were calculated with and without weighting. For both scoring methods, some traits involved continuous variables for which no species-specific vulnerability thresholds were established (e.g., low environmental heterogeneity within distribution range). For these variables, species with trait values in the lower quartile across values were scored as having 'high' vulnerability for that trait. Finally, we adapted a framework from Zhang et al. (2019) and used this together with the ordinal and additive scores to divide species into one of five climate change vulnerability categories: Unknown vulnerability, Low vulnerability, Moderate vulnerability, High vulnerability and Very High vulnerability (Figure 1). It is important to note that the use of this calculation method means that the vulnerability of the species is relative to the focal group and cannot be compared with other assessments.

An area of concern with trait-based methods is that the number of species categorized as vulnerable generally increases as the number of traits included increases (Hossain et al., 2019). Additionally, some traits may have disproportionate influence on the findings because the values/criteria set to define the trait's presence are too broad and cover the majority of species within the assessment. We therefore used a sensitivity analysis to examine the influence of individual traits on the overall ordinal score of each species. The species was assessed repeatedly with a different trait singly removed each time. The scores of each assessment in the sensitivity analysis were then compared to ascertain the influence of each trait (See S3 for results of the analysis).

2.3 | Use of vulnerability scores for spatial management

Distributions of vulnerable species were overlaid to create a raster layer representing numbers of species vulnerable

TABLE 2 Traits used to score amphibian vulnerability, the variables and vulnerability thresholds used to score each trait, and n, the number of species classified as high, low and unknown for each trait and threshold

Sensitivity					
Trait set[a]	**Traits**	**Weighting**[b]	**Variable to score**	**Vulnerability threshold**	***n***
A	AS1: Habitat specialization	Medium	Number of vegetation types present in species' range (South African Biodiversity Institute 2012)	High = Species range occurs within only one vegetation type	0
				Low = Species range occurs within >1 vegetation type	18
A	AS2: Microhabitat specialization	High	Number of microhabitat types used by the species (Torrents; Temporary water (Puddles, Vleis/Pans); Seeps; Lake/Estuarine systems; Permanent Water (excluding torrent); Terrestrial; and Garden Ponds)	High = Species relies exclusively on one microhabitat (excluding garden ponds) or is associated with temporary water, seeps, or terrestrial microhabitats	11
				Low = Species occurs in multiple microhabitats including torrents, lake/estuarine systems, permanent water (excluding torrent), or garden ponds	7
A	AS3: High elevation specialist[c]	Low	Minimum elevation at which the species occurs	High = Species is found only within top 20% of highest mountain peak	0
				Low = Species occurs at a range of elevations	18
B	AS4: Narrow temperature tolerance (adults)[c]	High	Average absolute deviation in temperature across the species' historical range	High = Lowest 25% (value)	5
				Low = Highest 75% (value)	13
B	AS5: Narrow precipitation tolerance (adults)[c]	High	Average absolute deviation in precipitation across the species' historical range	High = Lowest 25% (value)	5
				Low = Highest 75% (value)	13
B	AS6: Intolerant of changes to fire regime	High	Evidence of fire-based mortality and/or fire listed as a threat in the IUCN Red List	High = Evidence of fire-based mortality and/or listed as a threat in the IUCN Red List	2
				Low = Affected by lack of fire or associated with habitat less affected by fire	13
				Unknown = Uncertain	3
B	AS7: Sensitive to decline in cloud/fog cover	High	Evidence of the species' reliance of cloud cover/fog to remain within its environmental tolerances	High = Published evidence or expert expectation	6
				Low = Species' activity not limited by presence of cloud cover or fog	6
				Unknown = No understanding	6
B	AS8: Tadpoles reliant on highly oxygenated water bodies (fast flowing streams)	High	Evidence that tadpoles are restricted to highly oxygenated waters	High = Tadpoles reliant on fast flowing streams	1
				Low = Tadpoles not reliant on fast flowing streams	17
C	AS9: Dependent on environmental cues predicted to be disrupted by climate change	High	Evidence of dependence on rainfall or temperature cues to initiate breeding and/or migrating	High = Evidence found	16
				Low = Species uses environmental cues unaffected by climate change (e.g., photoperiod)	2
D	AS10: Narrow diet breadth	Low	Evidence of species having high dietary specialization (morphologically and/or physiologically determined)	High = Species relies on one species for the majority (>90%) of its food resources	0
				Low = Species consumes a wide variety of food types	14
				Unknown = No information	4
E	AS11: Endemic/rare	High	Endemic to Endemic to Table Mountain National Park (TMNP), Cape Floristic Region (CFR), South Africa (South Africa), southern Africa, Africa or multiple continents	High = Species is endemic or near endemic (within 10 km) to TMNP	4
				Low = Endemic to CFR, SA, southern Africa, Africa or multiple continents	14

(Continues)

TABLE 2 (Continued)

Sensitivity					
Trait set[a]	Traits	Weighting[b]	Variable to score	Vulnerability threshold	n
F	AS12: Limited to a single annual reproductive event	High	1. Maximum number of clutches per year	High = Reproduce ≤1 per year and timing limited to specific periods.	10
			2. Ability to reproduce at any time of year	Low = Can breed >1 per year at anytime	8
F	AS13: Eggs laid in leaf litter, moss, ephemeral water sources	High	Evidence the species is restricted to laying in leaf litter, moss, or ephemeral water sources	High = Species restricted to laying in leaf litter, moss, or ephemeral water sources	8
				Low = Species is not restricted to the laying environments described in the high threshold.	10
Low Adaptive Capacity					
G	AL1: Dispersal limited by physical barriers	High	Location of species' distribution relative to Cape Agulhas (Africa's southern tip)	High = The species' entire distribution is within 10 latitudinal degrees to the most southerly point of Africa	9
				Low = Species distribution covers >10 degrees of latitude	9
H	AL2: No commensalism with humans	High	Evidence of ability to use human dominated landscapes	High = Species is sensitive to anthropogenic modification of its environment	9
				Low = Evidence that the species is able to move through and use human dominated landscapes	9
I	AL3a and AL3b: Low microevolutionary potential	High	a. Mean annual reproductive output	High = ≤2 offspring per year	0
				Low = Evidence contradictory to that of high threshold	17
				Unknown = No information	1
		High	b. Genetic diversity and the degree of population fragmentation	High = Evidence of low genetic diversity within populations, and/or highly fragmented populations (b)	8
				Low = Evidence contradictory to that of high threshold	8
				Unknown = No information	2
I	AL4: Long generation time	High	Time to complete metamorphosis to adult form.	High = ≥12 months	1
				Low = <12 months	12
				Unknown = No information	5

[a]Trait set: A. Specialized habitat and/or microhabitat requirements; B. Narrow environmental tolerances or thresholds that are likely to be exceeded due to climate change at any stage in the life cycle; C. Dependence on a specific environmental trigger or cue that is likely to be disrupted by climate change; D. Dependence on interspecific interactions which are likely to be disrupted by climate change; E. Rarity; F. Sensitive life history; G. Poor dispersal ability; H. Limited behavioral adaptation; I. Poor evolvability.

[b]Expert weighting refers to the degree of relative importance a trait has on the sensitivity or adaptive capacity of a species when considered independently from the other traits.

[c]Allocated arbitrary thresholds due to the absence of empirical data for biologically meaningful thresholds.

to climate change. This method was repeated for the distributions of species assigned Very High, High and Moderate Vulnerability. All polygons were rasterized to a resolution of ~40 m^2 in R ver. 3.6.3, using the package “Raster” (Hijmans, 2020). Maps displaying the numbers of climate change vulnerable species across the study area were created for reptiles and amphibians using QGIS ver. 3.12.3. Finer spatial resolution was obtained for amphibian distribution maps due to the more extensive knowledge and data of amphibian breeding habitats and distributions within the park when compared to reptiles.

2.4 | Comparison to current IUCN Red List statuses

To explore whether already-threatened species are also likely to be climate vulnerable, we compared current IUCN Red List assessments, which did not explicitly

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consider climate change vulnerability, with our CCVAs. A Spearman's rank correlation was run using the "spearman.test" function in the R package *pspearman* (Savicky, 2014). For the purpose of the test, both climate change vulnerability and IUCN Red List statuses were assigned numerical values according to increasing levels of risk (IUCN: Least Concern = 1, Near-Threatened = 2, Vulnerable = 3, Endangered = 4, Critically Endangered = 5; Climate Change Vulnerability: Low = 1, Moderate = 2, High = 3, Very High = 4).

3 | RESULTS

3.1 | Missing data

For reptiles, data gaps were most acute for the tolerance of species to fire regime changes (RS6, 46% of species missing data), presence of semelparity (RS12, 24%), and whether they are limited to a single seasonal reproductive event (RS13, 17%). For amphibians, data gaps were most acute for species' sensitivity to change in cloud and fog cover (AS7, 33%), tadpole generation time (AL4, 28%), diet breadth (AS10, 22%), and tolerance to fire regime change (AS6, 17%). For all other traits, data gaps occurred for less than 15% of species.

3.2 | Sensitivity traits and scores

A total of 36 reptile species (88%) had at least one attribute that heightened their sensitivity to climate change (Table 1). The most frequent trait causing reptiles to be sensitive is having a single seasonal reproductive event (RS13) (22 species, 54%). All other traits were associated with 11 or fewer species, with the most common of these including narrow temperature and precipitation tolerances and low environmental heterogeneity (n = 11). The following traits were not found in any focal reptile species: habitat specialization (RS1), microhabitat specialization (RS2), high elevation specialist (RS3), narrow diet breadth (RS10) and rarity (RS11).

A total of 16 amphibian species (89%) had at least one attribute that heightened their sensitivity to climate change (Table 2). High reliance on environmental cues predicted to be disrupted by climate change (AS9) is a key concern for this group. Aside from strong microhabitat preference, all other traits were associated with 10 or fewer species. Habitat specialization (AS1) and high elevation specialization (AS3) were not present in any focal species.

3.3 | Adaptive capacity

A total of 35 reptile species (85%) was considered to be constrained in their ability to adapt to climate change (Table 1). Lack of commensalism with humans (RL2) is a key trait limiting adaptive response (n = 31). Low microevolutionary potential because of low genetic diversity and/or severe population fragmentation (RL4b) was identified in 11 species. No species were shown to have dispersal limitations due to physical barriers (RL1).

For amphibians, 12 species (67%) were constrained in their ability to adapt to climate change (Table 2). Dispersal limitation by physical barriers (AL1) and lack of commensalism with humans (AL2) was identified for 50% of species. Low microevolutionary potential because of low genetic diversity and/or severe population fragmentation (AL3b) was identified in eight species. No species were scored as having an annual reproductive output of two or fewer offspring.

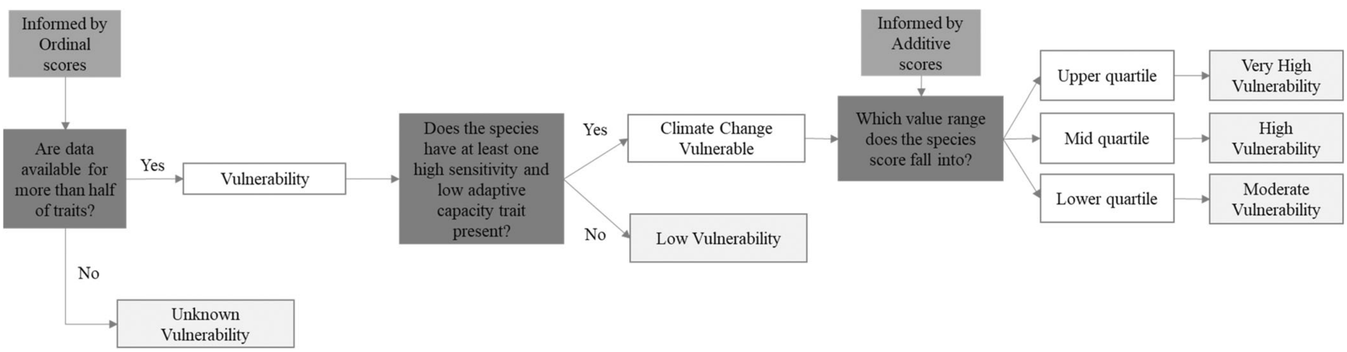

FIGURE 1 A framework for assessing species' vulnerability to the impacts of climate change (adapted from Zhang et al. (2019)). The five vulnerability categories identified are shaded in light gray

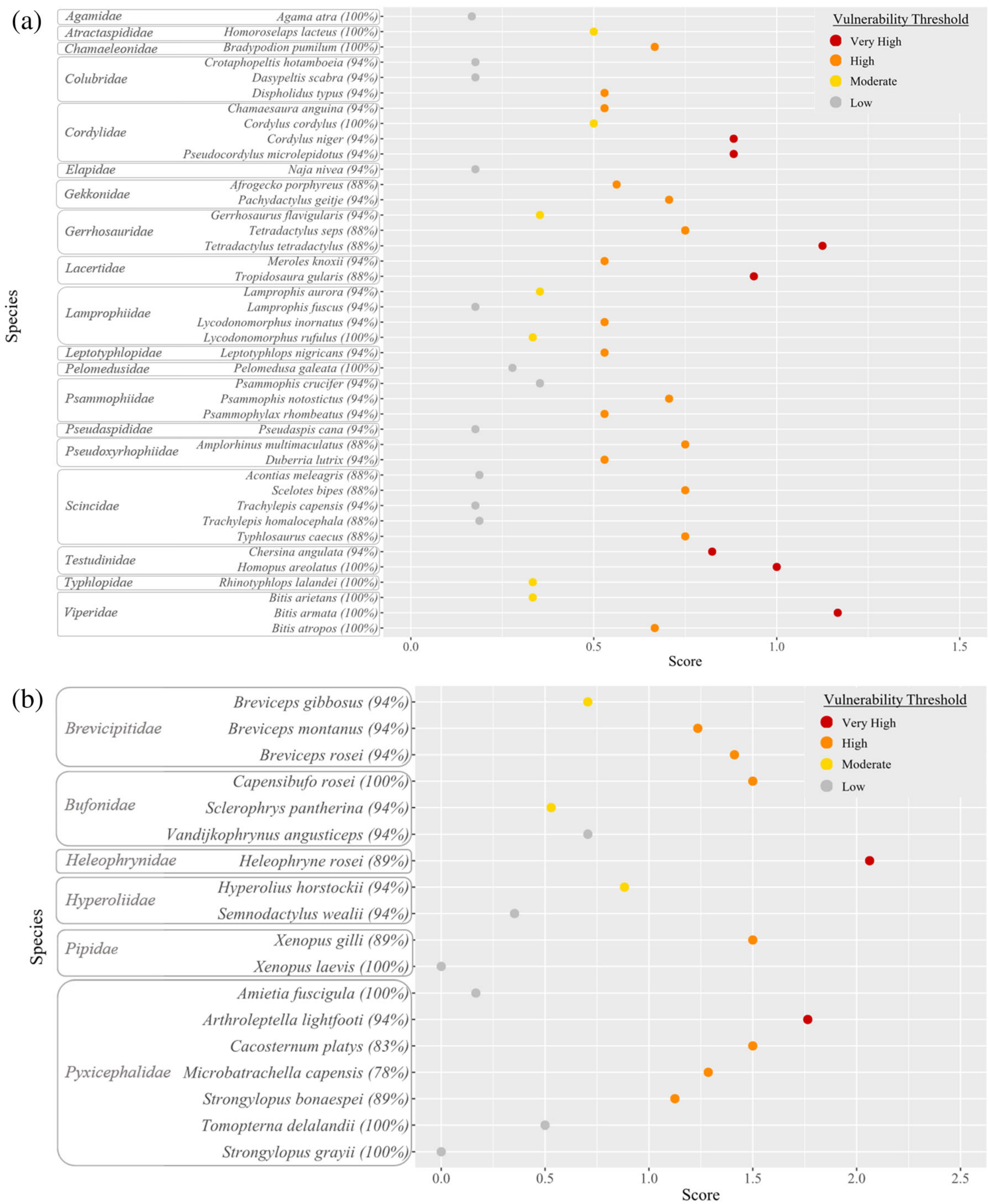

FIGURE 2 Climate change vulnerability categories and scores for (a) each focal reptile species ($n = 41$), and (b) each amphibian species ($n = 18$) within the study area according to the additive weighted scoring system. Colors indicate species' vulnerability determined by the assessment framework which combines the ordinal and additive scoring methods. Species are grouped by family in alphabetical order. The percentage of traits for which data were available is shown in brackets after species' names

3.4 | Summary of the overall vulnerability scoring

3.4.1 | Reptiles

All species had data for at least half of the traits assessed. Overall, 30 species (73%) had at least one trait reflecting high climate change sensitivity, and one adaptive capacity constraint. Among the vulnerable species, seven were identified as having Very High, 16 High and seven Moderate vulnerability scores. The most sensitive species overall (additive weighted score) were the southern adder (*Bitis armata*, 1.17), Cape long-tailed seps (*Tetradactylus tetradactylus*, 1.13), parrot-beaked dwarf tortoise (*Homopus *areolatus*, 1), Cape mountain lizard (*Tropidosaura gularis*, 0.94), black girdled lizard (*Cordylus niger*, 0.88), Cape crag lizard (*Pseudocordylus microlepidotus*, 0.88*)* and angulate tortoise (*Chersina angulata*, 0.82) (Figure 2a).

3.4.2 | Amphibians

All species had sufficient data to assess at least half of the traits within the framework. Twelve of the 18 amphibian species (67%) were identified as being vulnerable to climate change (Figure 2b). Among these, two had Very High, seven High and three Moderate vulnerability scores. The Critically Endangered Table Mountain ghost frog (*Heleophryne rosei*, 2.06) and Near Threatened Lightfoot's moss frog (*Arthroleptella lightfooti*, 1.77) were identified to have Very High vulnerability to climate change in relation to the other focal species assessed (Figure 2b).

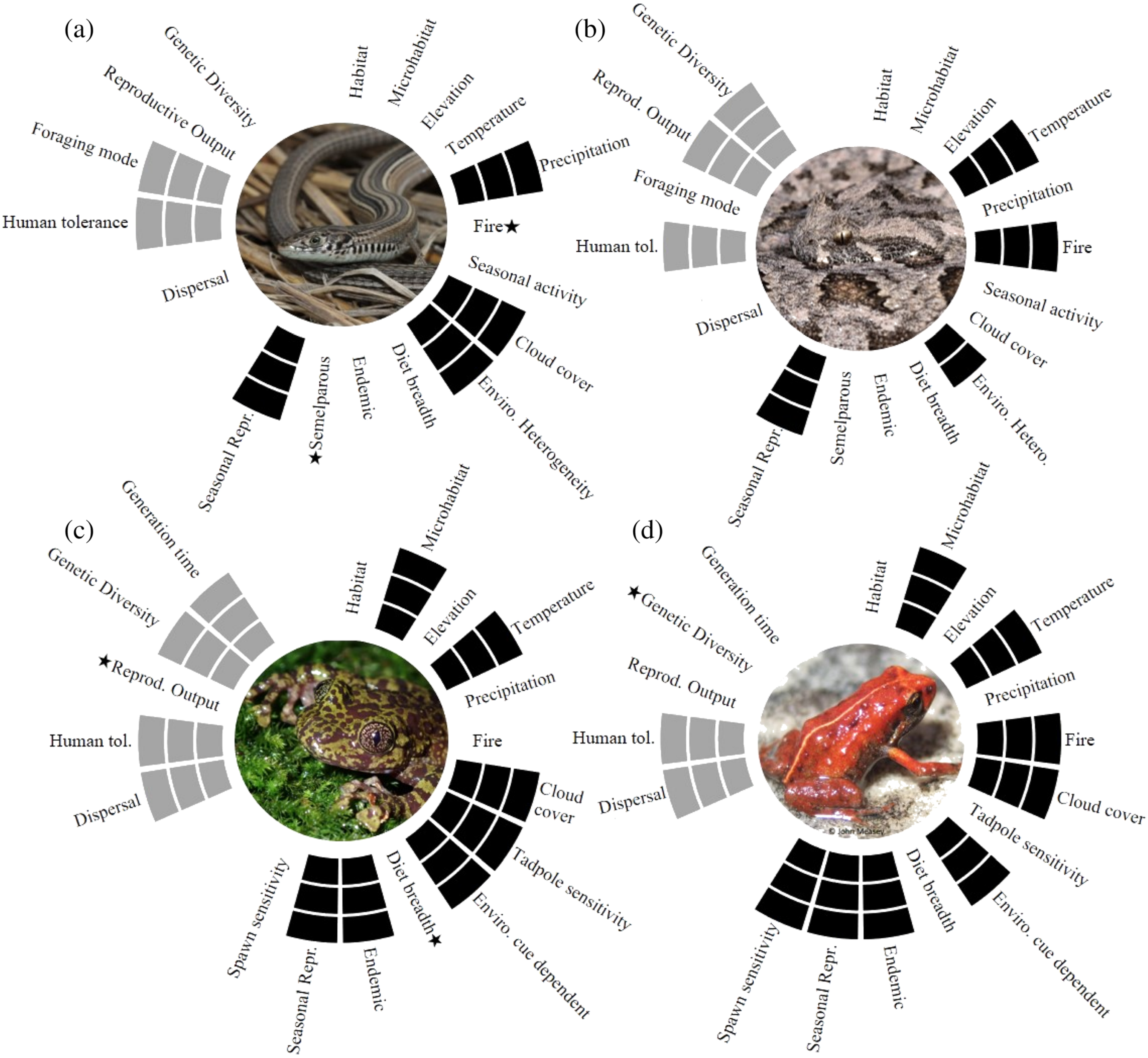

FIGURE 3 Traits conferring climate change vulnerability of the two most vulnerable species from each focal group: Reptiles - cape long-tailed seps (*Tetradactylus tetradactylus*) (a) and southern adder (*Bitis armata*) (b); amphibians - Table Mountain ghost frog (*Heleophryne rosei*) (c) and Lightfoot's moss frog (*Arthroleptella lightfooti*) (d). The number of widgets highlights the weighting of the trait (e.g., 3 widgets indicate the trait contributed a value of three to the species overall score. An absence of widgets indicates the trait was not present in the species). Black widgets indicate climate change sensitivity traits, while gray widgets indicate low adaptive capacity traits (Tables 1-2 and supporting information). A star indicates absence of information for a particular trait. Photo credits: Alex Rebelo (a), Tyrone ping (b), Josh Weeber (c) and John Measey (d)

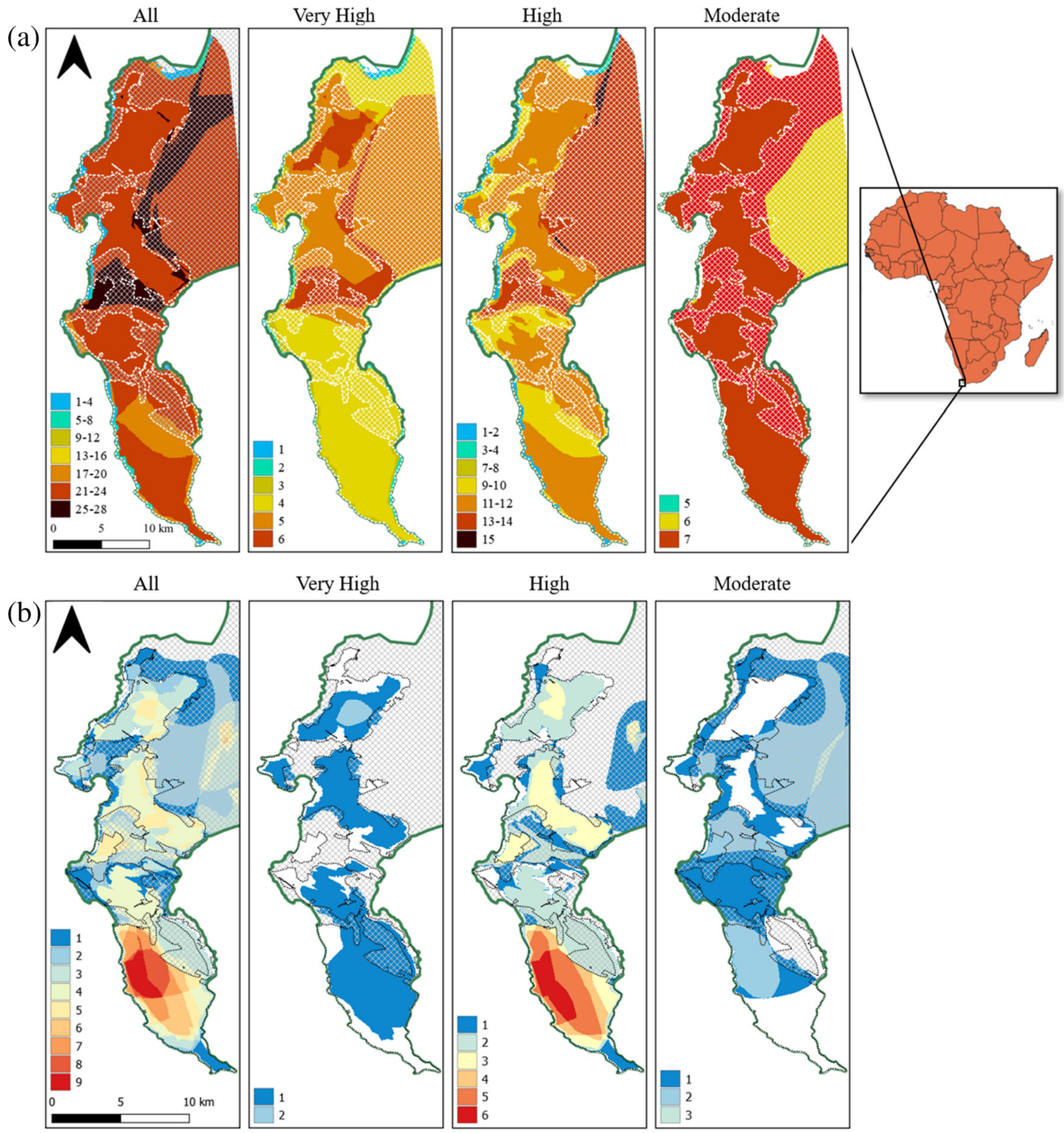

FIGURE 4 Numbers of climate change vulnerable (a) reptile ($n = 34$ of 40 species assessed) and (b) amphibian ($n = 12$ of 18 species assessed) species across the study area separated into: All vulnerable species, and those scored as having very high, high and moderate vulnerability. Hatched areas are outside of Table Mountain National Park

3.4.3 | Traits present in the most vulnerable species

The reptile assessment indicated that the southern adder was the most climate change vulnerable reptile species among the focal community. Traits that increased the sensitivity of the southern adder to climate change included narrow temperature tolerance (RS4), intolerance of changes to fire regimes (RS6), low environmental heterogeneity within its range (RS9) and its single annual or biennial reproductive event (RS13). The southern adder was also identified to have poor adaptive capacity because it is unable to use human-dominated landscapes (RL2) and has low microevolutionary potential (RL4a and RL4b) (Figure 3). The Cape long-tailed seps was scored Very Highly Vulnerable (VHV) due to narrow precipitation tolerances (RS5), reliance on fog/cloud cover (RS8), low environmental heterogeneity within its distribution (RS9), and a single annual reproductive event (RS13). This species' inability to use human-dominated landscapes (RL2) and a foraging mode that limits behavior adaptation reduces its adaptive capacity (RL3; Figure 3). The five other species were classified as VHV, based on similar combinations of traits. The angulate tortoise had a seasonal activity period restricted by temperature (RS7), not seen in any of the other six very vulnerable reptile species.

The climate change sensitivity of the Table Mountain ghost frog and Lightfoot's moss frog were driven by microhabitat specialization (AS2), narrow temperature tolerances (AS4), sensitivity to declines in cloud/fog cover (AS7), dependence on environmental cues predicted to be disrupted by climate change (AS9), being endemic/rare (AS11) and their single annual reproductive event limited by environmental conditions (AS12) (Figure 3). Dispersal limitation by physical barriers (AL1) and lack of commensalism with humans (AL2) was also identified to decrease their adaptive capacity. The Lightfoot's moss frog was assessed as intolerant of changes to fire regime (AS6), and has eggs laid in leaf litter, moss and/or ephemeral water sources (i.e., desiccation-prone nesting habitat) (AS13). The Table Mountain ghost frog was also climate change vulnerable; its tadpoles are reliant on highly oxygenated water (AS8) and have long generation length (AL4), and the species is assumed to have constraints on genetic diversity due to its small population size and highly restricted range (AL3b) (Figure 3).

3.4.4 | Spatial analysis

Aside from the coastal edges of the park, the peninsula is homogenous in terms of the presence of vulnerable reptile species. The majority of the park has between 25 and 28 vulnerable reptile species. The central lowland areas of the park appear to have the greatest number of climate change vulnerable reptile species (28, Figure 4a - All). The central and eastern fringes of the park contain five of the seven VHV species (black-girdled lizard, angulate tortoise, parrot-beaked dwarf tortoise, Cape long-tailed seps, and Cape crag lizard) (Figure 4a - Very High). In addition, the higher elevation areas of the northern section of the park are also within the distribution of six of the seven VHV reptile species (Cape mountain lizard, black-girdled lizard, angulate tortoise, parrot-beaked dwarf tortoise, Cape long-tailed seps and Cape crag lizard; Figure 4a - Very High).************

For amphibians, the greatest diversity of climate-change-vulnerable species exists in the southern section of the park (nine species, Figure 4b - All). This section contains six of the seven species classified as Highly vulnerable (HV) (Rose's mountain toadlet (*Capensibufo rosei*), mountain rain frog (*Breviceps montanus*), Rose's rain frog (*Breviceps rosei*), flat caco (*Cacosternum platys*), banded stream frog (*Strongylopus bonaespei*) and Cape platanna (*Xenopus gilli*) (Figure 4b - High)). However, the most highly vulnerable species, the Table Mountain ghost frog, occurs exclusively on Table Mountain, located in the northern section of the park (Figure 4b – Very High).

3.4.5 | Comparison between trait-based assessments and IUCN Red List statuses

There was no significant correlation between the IUCN Red List status and our trait-based assessments (weighted) for reptiles ($r = 0.225$, $p = 0.156$). However, the CCVA scores for amphibian species were positively correlated with IUCN status ($r = 0.557$, $p = 0.018$; see SI1 for correlations of unweighted scores).

4 | DISCUSSION

We present an approach for conservation practitioners that is tailored for carrying out rapid multispecies assessments of climate change vulnerability at small spatial scales that normally preclude the use of methods that rely on species distribution modeling. We describe its application to the herpetofauna of TMNP and the use of its outputs to park managers. This trait-based CCVA framework highlights the TMNP reptile and amphibian species that are likely to be most at risk from climate change and offers insights into the mechanisms underpinning likely impacts. High climate change vulnerability was found for 73% of reptile and 67% of amphibian species, based on the presence of both high sensitivity and low adaptive capacity traits. In combination with spatial representation of high concentration areas of climate change vulnerable species, these findings provide valuable and practical information that may be used to guide climate change response strategies both within and beyond PAs.

For amphibians, higher climate change vulnerability was matched by IUCN Red List statuses of greater threat. Since the current IUCN Red List assessments of these species have not incorporated climate change vulnerability, the match between current Red List status and climate change vulnerability likely reflects overlap between traits associated with higher risk from climate change and those of non-climatic stressors. This highlights the risk that already-threatened species, some potentially on the brink of extinction, may face additional climate change stressors that are not covered by existing conservation plans, and additional measures (e.g., ex-situ conservation) may be needed. For reptiles, however, increasing climate change vulnerability was uncorrelated with higher Red List status. Since conservation prioritization within the park has previously focused on non-climatic threats alone, threats to these species may not be covered by existing conservation measures. As concluded from an assessment of global fishes (Nyboer et al., 2021), assessing climate change vulnerability of individual species can reveal large mismatches in current conservation efforts and degrees of climate change vulnerability.

In TMNP, spatial representation of CCVAs (e.g., vulnerability "hotspots"), in combination with existing ecological layers (e.g., park sensitivity, use zones, habitat representation and priority areas for alien clearing) is being used to provide better representation of conservation needs in the park. For example, the Table Mountain area is within the distributions of six of the seven reptile species, and both amphibian species deemed to have Very High climate change vulnerability (Figure 4a – Very High and 4b – Very High). Although cross-taxonomic group comparisons of absolute vulnerability cannot be made, identifying areas where the proportions of each group's climate vulnerable species are greatest allows for comparisons of spatial prioritization and protection. This information, used in conjunction with the park's other spatial layers, will assist to: appropriately zone the park for tourist use such that footpaths and infrastructure are avoided or diverted in high-diversity areas; aid in the prioritization of areas for alien species removal; and identify where existing roads and tourism infrastructure impact on connectivity between hotspots. For example, many toads are killed on roads during breeding and appropriate under-passes may be useful (Schmidt et al., 2020).

Since TMNP covers a small geographic area and most of its reptile species have relatively large global distribution ranges, and hence, largely overlap, we found that distinguishing 'hotspots' from surrounding areas challenging (Figure 4a). Several amphibian species, however, are restricted to specific microhabitats, leading to discrete areas of distributional overlap and clear 'hotspots'. We therefore recommend consideration of the relative sizes of the protected (or other assessment) area and of the range sizes of prospective assessment species before attempting to use this assessment approach to identifying spatial priorities.

Identifying life history traits associated with increased vulnerability (e.g., microhabitat specialization) both from climate change and anthropogenic pressures, can help to explore the likely mechanisms of climate change impact. For example, the breeding success of Rose's mountain toadlet seems to be associated with the presence of open vegetation around ephemeral pools, since these allow for pools of sufficient size, depth and temperature to form (Edwards et al., 2017). Disturbance of vegetation, e.g., from natural fires or herbivory, likely benefits the species by creating open habitat conditions for breeding. However, adults also appear to require animal burrows which provide refuge from dry summer weather, and during wildfires (Measey et al., 2021). Substrate compaction from high human footfall could compromise burrows, reducing the species' capacity to deal with predicted climate change-driven increases in fire frequency and intensity (van Wilgen & Herbst, 2017). In addition, where fire suppression is required as a result of the urban-wildland interface, bush encroachment creates sub-optimal breeding conditions. Understanding the nexus of impacts of both climate change and current management policy (e.g., on fire or footpath use) can provide insights into where conservation intervention may be needed or adjusted.

Identifying and exploring observed and predicted impact mechanisms frequently exposes gaps in species and ecological knowledge and, as such, exposes monitoring and research needs. There is a need for further research into the tolerances of TMNP species to changes in fire regimes and cloud cover, reproductive strategies, genetic diversity among populations, and the benefits and/or penalties of fossorial specialization, particularly among focal reptile species. In TMNP, local population density of Lightfoot's moss frog within a subsection of the park has been estimated using acoustic, spatially explicit capture-recapture (aSCR) (Measey et al., 2017). Informed by spatial outputs from our assessment, the need for wider use of aSCR and Spatial capture–recapture for monitoring population trends and intervention success is clearly apparent, for both the Lightfoot's moss frog and other species identified to be climate change vulnerable in this study (Measey et al., 2019; Muñoz et al., 2016).

Although a trait-based approach was arguably the best method for the scope of this study, it is important to highlight challenges and caveats. We acknowledge that selection of traits is subjective and influences the outcomes of the assessment. Traits such as narrow temperature tolerance (RS4 and AS4), narrow precipitation tolerance (RS5 and AS4) and low environmental heterogeneity within a range (RS9) were allocated arbitrary thresholds for assigning vulnerability due to the absence of empirical data for biologically meaningful thresholds, but excluding these factors would misrepresent key climate change sensitivity characteristics. Assessments are therefore relative representations of vulnerability that may change if more or less stringent thresholds are chosen.

Following the methods outlined in Foden et al. (2013), changes in arbitrary thresholds by -10% and $+10\%$ saw similar proportional changes in the number of species categorized as high risk for these traits (S3). Related to this, the number of species identified as vulnerable is relative to the individual framework and set of focal species present and, therefore, the amphibian and reptile assessments described are not comparable. Including a broader area (resulting in more species) would also alter priorities. For example, we expected *Capensibufo rosei*, which has declined in TMNP despite PA status, to be one of the most vulnerable species (Cressey et al., 2014). However, it was classified as HV, while two other amphibians were classed as VHV. Additional research may provide insights into physical tolerance limits that this assessment may have overlooked. Our assessment has highlighted that several significant assumptions (e.g., the greater the number of vulnerability traits present the more likely that vulnerabilities will be detected) have to be made to carry out the approach.

Gaps in expertise and knowledge on herpetofaunal life histories, ecology, demographies and behavior pose challenges for all CCVA approaches, as well as for conservation of these species (Böhm et al., 2013). Even though herpetofauna are comparatively well studied in South Africa (Measey et al., 2019; Tolley et al., 2019), our assessment highlights key data gaps for CCVA's (data absent for >20% of species, in particular for traits such as the presence of semelparity in reptiles).

Despite the effects of data paucity, a key benefit of this method is that, as new information becomes available, updates can be easily made to species' vulnerability scores, reducing uncertainty (e.g., the micro-frog currently has no information for four traits). Soliciting information through expert consultation ensured that the best available knowledge of focal species, including unpublished data, was included. It also provided a platform for collaboration between herpetologists and managers, thereby promoting research on priority data gaps and improving science management collaboration. Uncertainty around the nature of climate change exposure also limits the evaluation of this key dimension of CCVA. In particular, while a significant degree of microhabitat variation is known to exist in this mountainous park, there are no accurate projections of climate change at this scale. While collecting fine-scale microclimate data across areas such as TMNP is a costly and time-consuming exercise, it may be possible to model small scale variation in this way as new technology becomes available (e.g., Bennie et al., 2008).

Using a trait-based approach that incorporates both ordinal and additive scoring methods at the scale of a single PA has emphasized that the use of an ordinal method alone is not advisable. The ordinal method identified 76% of reptile species in TMNP as vulnerable to climate change. When the majority of assessed species have vulnerability to climate change, the binary output (vulnerable vs. non-vulnerable) of the ordinal method limits its use in decision making, particularly when effort and funds require species prioritization. By examining finer-scale variance among these vulnerable species using an additive scoring method, we were able to offer an interpretation of interspecies variation in climate change vulnerability within the focal groups.

The development of focused conservation interventions that address species-specific causes of climate change vulnerability is key. For example, amphibian species that are climate change sensitive due to their reliance on small temporary puddles (AS2: see Edwards et al., 2017) could be maintained by artificially creating disturbances that reduce vegetation cover. This might allow populations to remain stable across drought and wet years. Species-specific climate change adaptation interventions are already being trialed in TMNP through the provision of insulated nesting boxes for African penguins to improve breeding conditions and reduce heatwave mortality (Foden et al., 2021). Such interventions, including those that target sensitive life phases, provide a robust approach to delivering tangible, on-the-ground benefits to individuals, subpopulations and species under climate change.

In combination with the identification of spatial "hotspots" of vulnerable species, aggregating species-level responses at site, habitat and landscape scales can provide valuable information for park-scale management planning. Overlaps and differences in highlighted areas and required interventions provide managers with insights into the various scales and spatial patterns at which monitoring and interventions need to take place, as well as into the trade-offs that may be needed between individual species' conservation requirements.

AUTHOR CONTRIBUTIONS

Jack Harper - Conception and design, collated data, designed and performed the analysis/assessment; wrote the paper. Nicola J. Van Wilgen, Wendy Foden - Conception and design, aided the acquisition of data, analysis and interpretation of data, and drafting and revising of the manuscript. Andrew Turner, Krystal Tolley, Bryan Maritz, Susana Clusella-Trullas, John Measey - Aided final assessment design, the acquisition of data, interpretation of data, and drafting and revising of the manuscript. Susan J Cunningham, Jessica M da Silva, Chad Cheney – Aided final assessment design, and drafting and revising of the manuscript. Atherton L De Villiers - Aided final assessment design, the acquisition of data, and interpretation of data.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this assessment are publicly available at https://doi.org/10.25375/uct.20021726

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SUPPORTING INFORMATION

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

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