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RESEARCH ARTICLE

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Winners and losers in a changing climate: how will protected areas conserve red list species under climate change?

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Abstract

Aim: A fundamental challenge to protected area-based conservation is that protected areas are typically established under assumptions of environmental stationarity. With a rapidly changing climate, this assumption of stationarity is violated, and climate change could push some species beyond the bounds of currently protected areas. Here, we evaluate the efficacy of protected areas in conserving threatened plant biodiversity under future climate projections.

Location: South Africa.

Methods: We use ensemble species distribution modelling to map the projected distribution of South Africa's ~1200 threatened endemic plant species under present-day and projected climate scenarios for 2050. We quantify the performance of the existing protected area network by examining changes in the relative proportion of species' projected geographic extents within protected areas. We then examine whether current IUCN Red List status is a good predictor of climate 'winners' and 'losers.'

Results: We find that 56%–66% of species may have a greater proportion of their projected range extent falling within protected areas in 2050 under climate scenarios of mitigated and upsurge greenhouse gas emissions (Representative Concertation Pathways 4.5 and 8.5). However, this increase in the proportion of range protected is frequently associated with range contraction outside of protected areas. We also show that current threat intensity is not a good indicator of which species will lose versus gain increased protection.

Main conclusions: Our results suggest that the existing reserve network is surprisingly robust to projected range shifts; however, we also identify regions where species protection needs to be improved. In addition, we suggest that there is an urgent need to better incorporate future climate threats into the assessment of species extinction risks.

KEYWORDS
climate change, conservation, endemism, species distribution modelling, threatened species

1 | INTRODUCTION

Climate strongly determines the distribution of habitats suitable for the establishment, growth and reproduction of plant species (Ackerly et al., 2010; Araújo & Rahbek, 2006; Kelly & Goulden, 2008; Williams et al., 2005). Climate change is now recognized as a major conservation concern, with recent studies predicting the expansion or contraction of suitable habitats for many taxa (Brown & Yoder, 2015; Cheung et al., 2015; Gillings et al., 2015; Renwick & Rocca, 2015; Rowe et al., 2015), shifts in phenology and demography (Ackerly et al., 2010), variation in productivity and growth (Midgley et al., 2002), and the potential for local extinctions under future climate scenarios (McLaughlin et al., 2002; Wiens, 2016; Williams et al., 2005). Throughout geological history, plants have been able to adapt to slowly changing climatic conditions. However, the rapid pace of recent climate change, averaging 0.27°C per decade since 1974 (Kelly & Goulden, 2008), may exceed the rate at which many plants can adapt or disperse to new environments (Ackerly et al., 2010; Heller & Zavaleta, 2009), and it is possible that climate change could transcend habitat fragmentation as the principal cause of species loss in the near future (Ayebare et al., 2018).

Protected areas are a mainstay in the battle against biodiversity loss (IUCN WCPA, 2013). However, a fundamental challenge to protected area conservation is that non-stationarity in climate could drive shifts in species composition, such that reserves might not encompass the same assemblage of species in the future as they do today (Monzón et al., 2011; Rutherford et al., 1999; Wang et al., 2016). The global fingerprint of climate change shows that, on average, species are migrating 6.1 km poleward every decade (Parmesan & Yohe, 2003; Richardson, 2008). Climate-driven range shifts are a particular threat to endemic species (Loarie et al., 2008; Malcolm et al., 2006; Wiens, 2016), as many are narrow range habitat specialists, with long life spans, low reproduction strategies and limited dispersal ability (Foden et al., 2009, 2013; Grime, 2006). Regions rich in endemic taxa could, therefore, be at risk of major biodiversity declines if current rates of climate change continue into the future. The endemic flora of the Wet Tropical Bioregion of Australia serves as an illustrative case study. Currently, the flora is well represented in the existing protected areas network, but suitable species habitats within protected areas are predicted to decline by between 17% and 100% by 2040 (Costion et al., 2015).

Here, we use species distribution models (SDMs) to evaluate the efficacy of the current protected areas network in safeguarding threatened endemic plants in South Africa under future climate scenarios. SDMs use information on the climate conditions where species are currently found to characterize species' environmental requirements, which can then be applied to forecast the distribution of species under future climate scenarios (Elith & Leathwick, 2009; Hijmans & Graham, 2006). Such models can provide important insight into which species may become threatened in the future, and also highlight areas that may face notable shifts in species distribution and composition with climate change (Ackerly et al., 2010).

South Africa is the most floristically species-rich country in Africa, with three global biodiversity hot spots: the Cape Floristic Region (CFR), the Succulent Karoo (SK) and the Maputo-Pondoland-Albany Region (MPAR) (Myers et al., 2000). These hot spots combined represent at least 13,000 plant species that are found nowhere else in the world (Raimondo et al., 2009). South Africa is already experiencing impacts of anthropogenic climate change. Over the past 50 years, the country has recorded high-temperature increases and extreme rainfall occurrences. Mean annual temperatures have increased 1.5 times the global average (Ziervogel et al., 2014), and average precipitation has increased by 2% (Heller & Zavaleta, 2009). As species shift in their distributions in response to these changes, there is uncertainty as to how the existing protected areas network will perform in safeguarding their futures. One early assessment suggested that up to 42% of species could become locally extinct from selected reserves as a consequence of changing climate (Rutherford et al., 1999).

We explore two different climate scenarios from the Intergovernmental Panel on Climate Change's (IPCC) Fifth Assessment Report based on policy-driven emission cuts of varying severity. The first (representative concentration pathway [RCP] 4.5) assumes global mean temperature change is kept to below 2°C – this warming threshold was set by scientists to avoid dangerous impacts of climate change in the future (Knutti et al., 2016). The second (RCP 8.5) has been referred to as the "business-as-usual" scenario, but represents a higher estimate assuming continued use of traditional fossil fuels with little mitigation before 2100 (Liddicoat et al., 2013). We use projected geographic extents from SDMs to examine whether currently threatened species will lose conservation protection under these two scenarios. We then identify key areas that represent likely conservation gaps in the future, which we highlight as priority areas for expanding the existing protected area network.

2 | METHODS

2.1 | Occurrence data

We compiled a list of threatened plant taxa for South Africa from the South African Red List database (Raimondo et al., 2009), identified as those falling within one of the following threat categories: Critically Endangered, Possibly Extinct (CR PE), Critically Endangered (CR), Endangered (EN) and Vulnerable (VU). We then used this species list to extract distribution data from a more comprehensive data set of all endemic plants for South Africa (for further details, see Hoveka et al., 2020). Since spatial predictions from species distribution models (SDMs) are influenced by the number of occurrence points, with accuracy decreasing as they are informed by less data, we only included species with five or more occurrences. Our final database consisted of >37,000 georeferenced records from >1200 species representing 77 families and 303 genera.

2.2 | Current and future environmental predictors

We extracted 19 raster-based bioclimatic variables from the WorldClim database (Hijmans et al., 2005) (http://worldclim.org), representing interpolated climate station records from 1950 to 2000 and projected future scenarios at a spatial resolution of 10 arc minutes, approximating the resolution of the species occurrence data. We used two different emission scenarios from the Intergovernmental Panel on Climate Change's (IPCC) Fifth Assessment Report (CMIP5) based on policy-driven emission cuts of varying severity: the 4.5 and 8.5 representative concentration pathways (RCPs) under the Hadley Centre Global Environmental Model, version 2, Earth System (HadGEM2-ES). This fully coupled Earth System Model explains how emissions might evolve through modifications in the terrestrial and ocean carbon stores, and primarily focuses on changes in vegetation distribution and the function played by vegetation in shaping emissions (Liddicoat et al., 2013). The HadGEM2-ES temperature simulations in Africa are similar to those of the National Center for Atmospheric Research (NCAR) for the period 1979–2004 and the annual cycles of temperature and precipitation using HadGEM2-ES converge on the multi-model ensemble mean in CMIP5 (Dike et al., 2015).

The 4.5 RCP assumes reduction in fossil fuel use (Knutti et al., 2016) based on agreements to limit global mean temperature change to below 2°C (Bodansky, 2016) at the 2015 climate conference in Paris. The 2°C warming target is a universally recognized limit set by scientists to avoid dangerous impacts of climate change in the future (Knutti et al., 2016). RCP 4.5 assumes 580–650 ppm CO^2 and 0.9–2.0°C increase by 2050 (Guisan et al., 2002; IPCC, 2013, 2014). RCP 8.5 is often referred to as a “business-as-usual” scenario and assumes the continued use of traditional fossil fuels with little mitigation before 2100 (Knutti et al., 2016); RCP 8.5 assumes >1000 ppm CO^2 and 1.4–2.6°C increase by 2050 (IPCC, 2013, 2014).

As sensitivity analyses, we additionally re-ran species distribution models using general circulation models (GCM’s) from The Max Plank Institute (MPI-ESM-LR: Block & Mauritsen, 2013) and the National Centre of Meteorological Research (CNR-CM5: Voldoire et al., 2013), under the same RCPs.

2.3 | Species distribution modelling

Following the methods in Hoveka et al. (2020), we used ensemble forecasts of three distribution modelling approaches: generalized linear models (Guisan et al., 2002), random forests (Breiman, 2001) and the gradient boosting machine (Friedman et al., 2000), as described in Hijmans and Elith (2013), to establish current and future climate suitability projections. We generated binary presence–absence maps for each species under each climate regime by combining model outputs, weighted by their AUC, and thresholded to maximize the sum of actual-positive rate and actual-negative rate (Manel et al., 2001). Models were fit using the spdep R-library (Bivand & Wong, 2018); for additional details, see Hoveka et al. (2020).

TABLE 1 Per cent of species predicted to experience an increase in the proportion of their range within protected areas by 2050 under the two climate scenarios of mitigated (RCP 4.5) and upsurge (RCP 8.5)

General circulation model	RCP 4.5 (%)	RCP 8.5 (%)
HadGEM2-ES	64	66
MPI-ESM-LR	61	59
CNRM-CM	56	56

2.4 | Comparison of current versus future climates

We calculated the proportion of each species' range falling within protected areas by overlaying the current protected area network (shapefile from the Department of Environmental Affairs’ Protected Areas Database: https://egis.environment.gov.za/) onto species' projected distributions. We then summed the number of occupied cells within (centroid within the bounds) and outside recognized protected areas. For each species, we calculated a Species Representative Index (SRI) to quantify the change in the proportion of projected range area falling within protected areas (PA) between current conditions and those projected for 2050 under RCPs 4.5 and 8.5 using the equation below:

$$\mathrm{SRI} = \frac{\text{Occupied cells in PA future SDM}}{\text{Total occupied cells future SDM}} - \frac{\text{Occupied cells in PA current SDM}}{\text{Total occupied cells current SDM}}$$

Negative values indicate that species are projected to have reduced climatically suitable habitat space within protected areas, while positive values indicate that species have expanded their suitable habitat space within protected areas. From the ensemble forecasts, we also calculated the difference in geographic extent (number of occupied cells) of projected distributions between current and future climate scenarios.

3 | RESULTS

We used species distribution models (SDMs) to calculate the proportion of species ranges projected to fall inside protected areas under present and future climates. From the HadGEM2-ES model, we found that a majority (64%–66%) of the species included in our analyses are predicted to experience an increase in the proportion of climatically suitable habitat within protected areas in 2050 under the two climate scenarios of mitigated (RCP 4.5) and upsurge (RCP 8.5) greenhouse gas emissions (Table 1). The fraction of species with ranges projected to become proportionally more protected under climate change was marginally greater under the RCP 8.5 ($n = 835$) than the RCP 4.5 ($n = 821$). Changes in the proportion of range extent with protected areas were highly correlated among GCMs (Figure S1), although the overall percentages of species showing increases in relative conservation protection were slightly lower (56%–61%), depending on the combination of GCM and RCP (Table 1). However, under RCP 4.5, fewer species are predicted to become extinct (projected climate space shrinks to zero) than under the RCP 8.5 scenario (n = 6 and 16, for RCP 4.5 and 8.5, respectively: Table 2, see Tables S1 and S2 for list of species projected to be lost). Both species projected to increase in their relative area under conservation protection and species projected to decrease in their relative area under conservation protection are mostly found within the three global biodiversity hot spots (Figure 1), which represent the most species-rich regions in the country.

Under both RCP scenarios, we find that there is no statistically significant trend for species to be more likely to contract or expand their ranges (RCP 4.5: $t = -1.51$, df = 1273, $p = .13$ and RCP 8.5: $t = -0.06$, df = 1272, $p = .95$, from a t-test examining the distribution of range expansion and contraction across all species). However, there is a significant negative relationship between change in proportion of range in protected area and range expansion (RCP 4.5: $r^2 = .09$, $p = <.01$ and RCP 8.5: $r^2 = .10$, $p = <.01$, from a regression of the change in proportion of the species range in protected area on the difference between current and future projected range sizes occupied by the species). While the relationship between change in the proportion of range protected and range contraction/expansion is significant, the correlation strength is relatively weak (9%–10% of variation explained; see Figure S2a,b); thus, some species that show a reduction in the proportion of their range in protected areas may experience a range expansion outside of protected areas, and some species that show an increase in proportion of their range falling within protected areas may experience an overall range contraction. We classify these alternative outcomes as follows (Figure 2):

- win–win—species that are projected to increase the proportion of range area under conservation protection and experience an overall expansion in projected range size;
- win–lose—species that are projected to increase in the proportion of range area under conservation protection, but experience an overall decrease in projected range size;
- lose–win—species that are projected to decrease in the proportion of range area under conservation protection, but experience an overall increase in projected range size;
- lose–lose—species that are projected to decrease in the proportion of range area under conservation protection, and experience an overall decrease in projected range size.

TABLE 2 Number species predicted to experience an increase (winners) or decrease (losers) in the proportion of their range within protected areas, and number predicted to become extinct (zero projected occupancy) by 2050 under the two climate scenarios of mitigated (RCP 4.5) and upsurge (RCP 8.5)

RCP 4.5			RCP 8.5		
Winners	Losers	Extinct	Winners	Losers	Extinct
821	447	6	835	423	16

We find the win–lose scenario to be the most common, with an appreciable number of species (n = 471–491) experiencing gains in the proportion of range protected as a consequence of projected range contractions outside of protected areas (Figure 3). However, the lose–lose scenario was least common (n = 119), and some species are projected to show both range expansion and increases in the proportion of range area under conservation protection (win–win).

For species for which we could model future distributions, current threat intensity is not a good indicator of whether species are climate winners or losers (RCP 4.5: $f = 1.58$, df = 3, $p = .193$ and RCP 8.5: $f = 1.55$, df = 4, $p = .186$, from an ANOVA examining the change in the proportion of a species' range in protected area and conservation status). The biggest losers, however, could be the threatened endemic species whose ranges could not be estimated because we lack sufficient data on their distribution (n = 891). These data-poor species are generally more threatened than species for which we have sufficient data to generate range projections ($p < .01$, from a t-test examining the weighted conservation indices of species with and without sufficient distribution data to fit SDMs).

4 | DISCUSSION

Using species distribution modelling and range projections for >1200 species, we explore the effectiveness of the current protected area network in conserving South Africa's threatened endemic flora under climate change projected for 2050—a realistic timeframe for conservation decision-making. We find that a majority (56%–66%) of species will likely have a greater proportion of their suitable climate space falling within protected areas in the future under the two climate scenarios of mitigated (RCP 4.5) and upsurge (RCP 8.5) greenhouse gas emissions. However, the increase in relative conservation protective coverage is frequently associated with projected range contraction outside of protected areas, and a notable minority of species are projected to experience range contractions and losses in conservation protection.

The distribution and threat status of endemic species are key components in the setting of national conservation priorities (Orsenigo et al., 2018). To date, our analysis is the largest taxonomic study on the threatened endemic species of South Africa. Broennimann and colleagues (Broennimann et al., 2006) performed analyses at a similar spatial scale, but considered fewer endemic species. Previous biome-level analyses suggest that the Succulent Karoo and Fynbos could lose up to 65% of the area representing optimal bioclimatic conditions, while arid vegetation cover could increase by 30% at the expense of the grassland biome (Midgley & Thuiller, 2011). The Cape Floristic Region (CFR) has also been a major focus of work exploring the impact of climate change on the country's indigenous plants (Bomhard et al., 2005; Midgley et al., 2002, 2003, 2006; Williams et al., 2005). Here, we used climate projection forecasts and species distribution models to examine how the preservation of threatened endemic plant diversity will be impacted in the future across all biomes.

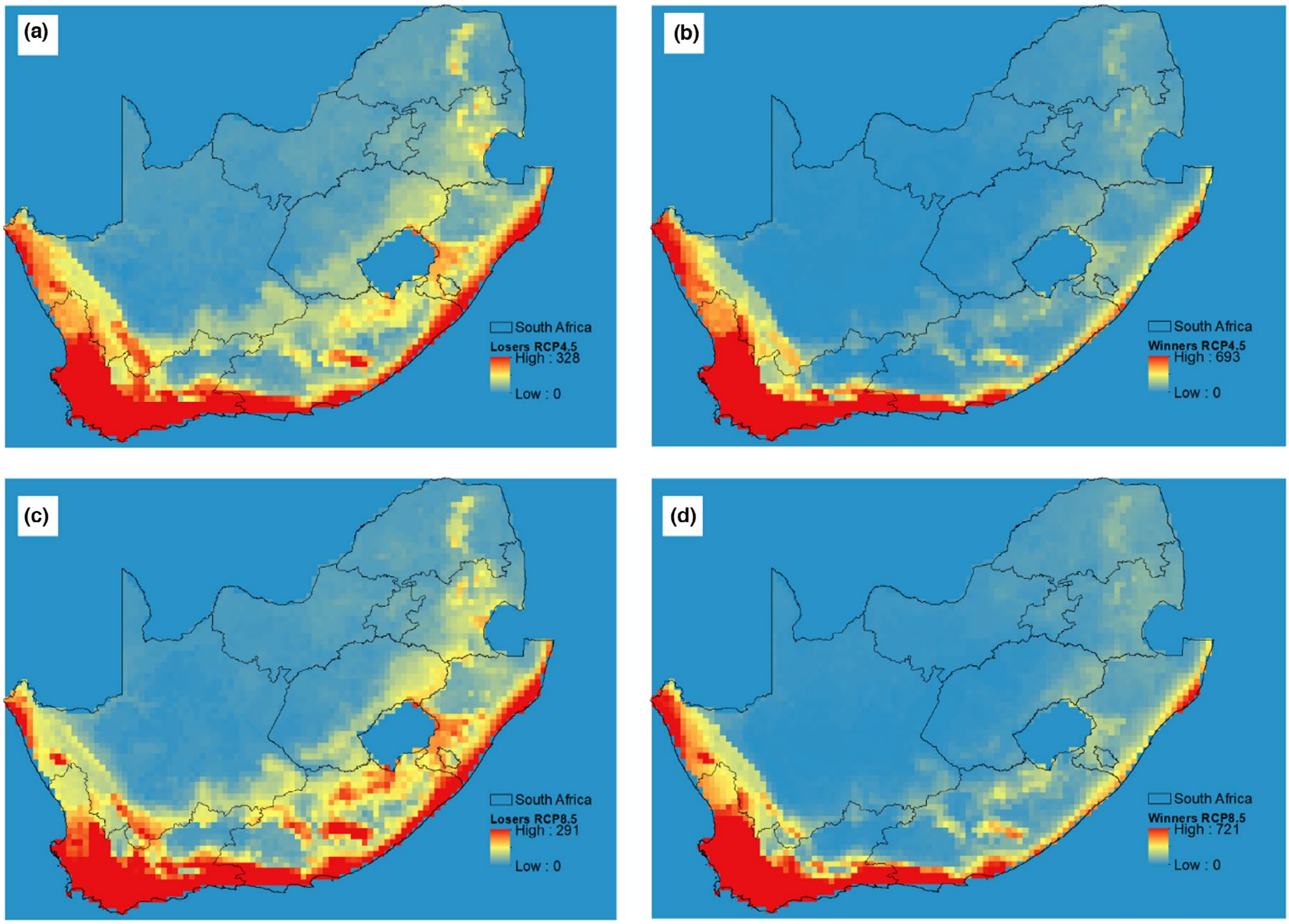

FIGURE 1 Predicted shifts in range distributions under projected climate change highlighting regions where threatened endemic species will experience conservation gains (increased proportion of ranges falling within protected areas) and where they will experience conservation losses (decreased proportion of ranges falling within protected areas): (a) richness of species experiencing conservation losses and (b) richness of species experiencing conservation gains under RCP 4.5; (c and d) provide maps matching to (a) and (b) under RCP 8.5. Red = high species richness, blue = low species richness

The use of species distribution models to predict future distributions has known limitations (Araújo & Luoto, 2007; Beaumont et al., 2005; Elith & Leathwick, 2009; Gotelli & Stanton-Geddes, 2015; Pearson & Dawson, 2003). We employed an ensemble forecasting approach to mitigate biases inherent in particular methods, and species distribution modelling remains the best approach for projecting species distributions when detailed information on the ecology and physiology of species is lacking (El-Gabbas & Dormann, 2018). Numerous studies have shown that species do indeed track their modelled distributions given sufficient time (e.g. birds (La Sorte & Jetz, 2015; Tayleur et al., 2015; Tingley et al., 2009), plants (Graham et al., 2010; Martínez-Meyer & Peterson, 2006), mammals (Rubidge et al., 2011; Santos et al., 2018) and species distribution models have been widely used to explore the efficiency of protected areas under future climate scenarios in many regions of the world (Araújo et al., 2011; Costion et al., 2015; Thuiller et al., 2006; Wang et al., 2016). However, as is the case for all species distribution models, our projections represent the extent of species' suitable climate space and do not necessarily represent species realized area of occupancy. Further, the accuracy of our results depends on the accuracy of both climate projections and species distribution models, and there is large uncertainty associated with both. While we therefore caution against over-confidence in projections, we believe the aggregate trends we present here may be less sensitive to species-specific idiosyncrasies, and we show they are robust to different RCPs and GCMs.

We identify species for which suitable climate space within protected areas will proportionally increase or decrease under climate change. Threatened and endemic species are thought to be, on average, more vulnerable to climate change. For example, it has been estimated that 34 endemic species in the Albertine Rift will lose 90% of their suitable habitat in the future (Ayebare et al., 2018), and in California, 66% of endemic species might lose more than 80% of their suitable habitat (Loarie et al., 2008). In South Africa, we show that climate-driven distributional shifts may increase the relative proportion of species' ranges under conservation protection for many threatened endemic species under both the moderate and extreme climate scenarios. However, this increase in proportion

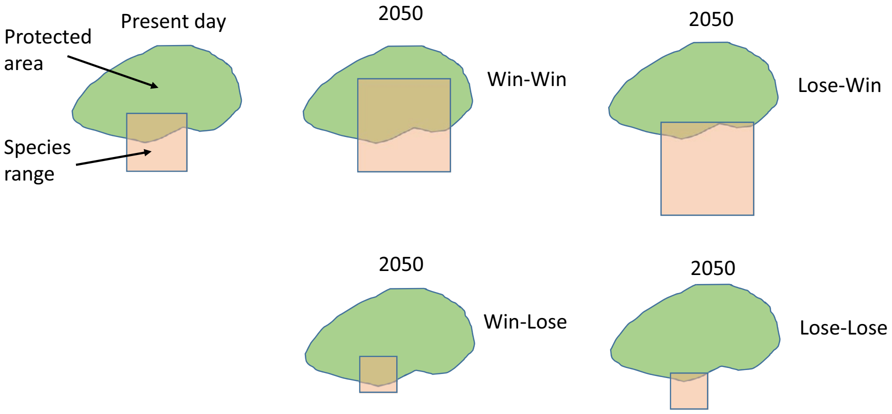

FIGURE 2 Cartoon illustrating alternative range dynamics that could explain climate winners and losers. Relative to its present-day range (far left), a species may be projected to: (top left) increase the proportion of range area under conservation protection and experience an overall expansion in projected range size (win–win); (bottom left)increase in the proportion of range area under conservation protection, but experience an overall decrease in projected range size (win–lose); (top right) decrease in the proportion of range area under conservation protection, but experience an overall increase in projected range size (lose–win); or (bottom right) decrease in the proportion of range area under conservation protection and experience an overall decrease in projected range size (lose–lose)

of projected range extent within protected areas is frequently associated with overall projected range contraction, indicating that many species may experiencing apparent conservation gains at the expense of overall geographical extent. We refer to this scenario as win–lose. Nonetheless, some species experience a win–win scenario, showing increases in both projected range extent and proportion of projected range area under conservation protection, and lose–lose scenarios (loss of range area and decrease in area under conservation protection) are relatively less common.

One explanation for shifts in species protection coverage under climate change is that the current distribution of protected areas does not accurately capture the diverse climate regimes across South Africa. For example, an over-representation of protected areas in arid regions and an under-representation of protected areas in wetter regions might favour drought-tolerant species at the expense of water-dependent species. A shift to warmer and drier climates could further exacerbate such inequities (see additional discussion in Hannah et al., 2007; Klausmeyer & Shaw, 2009). To explore this possibility, we examined the climate space encompassed by protected areas within South Africa relative to that encompassed nationally. We find that the climate space occupied by protected areas largely, if imperfectly, overlaps with the climate space of South Africa (Figure 4). We therefore suggest that the projected trends in species' protected area coverage might be better explained by the uneven distribution of species across climates rather than the uneven distribution of protected areas.

Our results indicating numerous conservation gains (win–win scenarios) for endemic species in South Africa are similar to observation from neighbouring Namibia, where a warmer climate is also projected to favour many endemic plant species (Thuiller et al., 2006). Notably, both countries are rich in plants that are preadapted to dry and warm environmental conditions, which could enable them to thrive in a drier and warmer world. Studies that have projecting species range contractions and losses frequently encompass more tropical and cooler climates (Araújo et al., 2011; Ayebare et al., 2018; Loarie et al., 2008; Patiño et al., 2016). Interestingly, some studies projecting climate impacts in warm and arid regions in Europe have also forecast a preponderance of range contractions (e.g. in Italy [Attorre et al., 2018] and Spain [Munt et al., 2016]), although they have tended to have a more limited taxonomic coverage, and perhaps the larger geographic extent of South Africa encompasses a greater climate space, providing more opportunity for species to show range expansions. These mixed predictions indicate that the biotic impacts of climate change may vary dramatically across biomes and biogeographic regions. However, we suggest that some of the biggest climate losers may be the threatened endemic species whose ranges could not be estimated because we lack data on their current distributions. We find that these data-poor species are generally more threatened than species for which we had sufficient data to project their geographic distributions, and it is possible that a lack of data may be indicative of their present-day rarity and need for conservation attention (Lomba et al., 2010).

Despite a growing body of research on the impact of climate change on the survival of species, it is still rarely incorporated directly into Red List assessments due, in part, to uncertainties associated with future projection (Attorre et al., 2018; Patiño et al., 2016). It is notable that we do not find current threat intensity to be a good predictor of whether species are winners or losers under future climate projections. The threat posed by climate change is thus not well-reflected in current IUCN threat status (Foden et al., 2019; Keith et al., 2014; Trull et al., 2018), and incorporating impacts of climate change into IUCN Red List assessments could alter the threat status of many endemic species (Trull et al., 2018). For example, it is possible that climate-induced range expansion might place some highly threatened species into lower threat categories, or range contraction could place species currently in low threat categories into a higher threat category (see Attorre et al., 2018). For instance, the critically endangered *Leucadendron globosum* (Kenn. ex Andrews) is

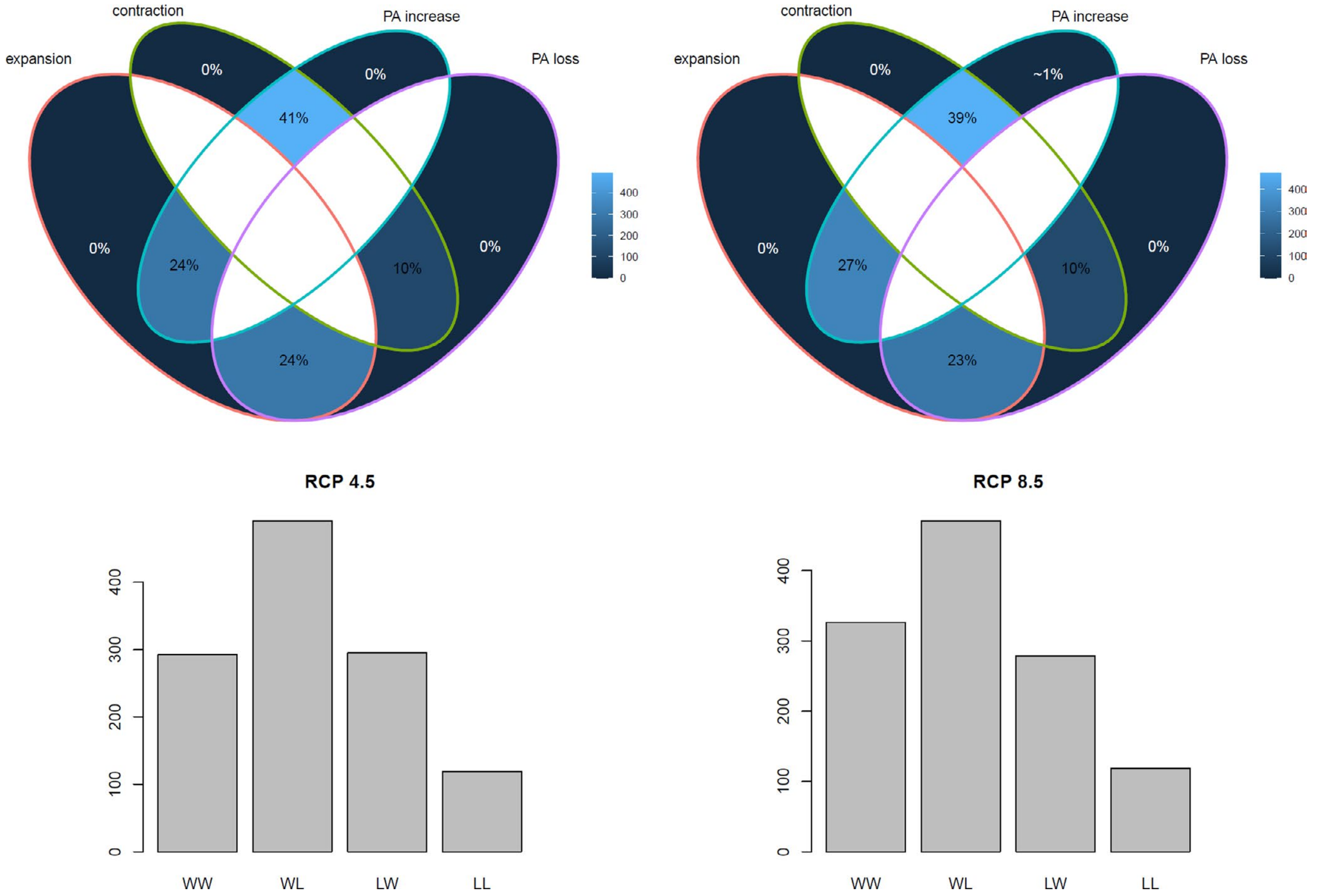

FIGURE 3 Venn diagrams and frequency distributions of species projected changes in range extent (expansion/contraction) and range area under conservation protection (PA increase/PA loss) for the 4.5 (left) and 8.5 (right) Representative Concentration Pathway assuming the HadGEM2-ES Global Climate model. WW (win–win)—species that are projected to increase in the proportion of range area under conservation protection and experience an overall expansion in range size. WL (win–lose)—species that are projected to increase in the proportion of range area under conservation protection, but experience an overall decrease in range size. LW (lose–win)—species that are projected to decrease in the proportion of range area under conservation protection, but experience an overall increase in range size. LL (lose–lose)—species that are projected to decrease in the proportion of range area under conservation protection, and experience an overall decrease in range size

predicted to be a climate winner, while the vulnerable *Leucadendron cinereum* (Sol. ex Aiton) is a climate loser. Kaky and Gilbert (2019) suggest that such information could be used to help inform extinction risk assessments for unassessed species, especially when other data are sparse and resources are limited, as in many developing countries. However, care must be taken when applying IUCN Red List criteria (Hannah, 2012), and estimating the timeframe over which extinctions may occur remains challenging (Kaky & Gilbert, 2019).

Our results indicate that, under future climate scenarios, the current protected areas network may be well positioned, such that more species are predicted to experience a gain in the proportion of their range protected than a decreases in the proportion of their range protected. However, the total geographic extent of many species is projected to decrease with climate change, and we identify regions where species protection needs to be improved. Notably, species projected to experience a decrease in relative protected area coverage (lose–lose and lose–win scenarios) tend to be concentrated in the interior of the country within the Nama Karoo and the Grassland biomes, where fewer protected areas exist (see Hoveka et al., 2020). We suggest that new or expanded protected areas need to be established to serve these species, safeguarding climatic refugia and currently under-represented habitats that could be key conservation areas in the future.

Our current models do not consider the numerous factors that could aggravate the projected impacts of climate change, such as specialization to restricted soil types, the spread of invasive species, genetic limitations on adaptive response, pollinator availability, propagule dispersal and disruption of natural fire regimes (Costion et al., 2015; Loarie et al., 2008; Midgley & Thuiller, 2011; Schierenbeck, 2016). Advances in species distribution modelling that allow these factors to be included directly into models, or alternative approaches, for example, using cellular automaton models (Attorre et al., 2018), might allow more accurate predictions of species movement across a changing landscape. Our analysis quantifies the geographic extent of species' suitable climate space,

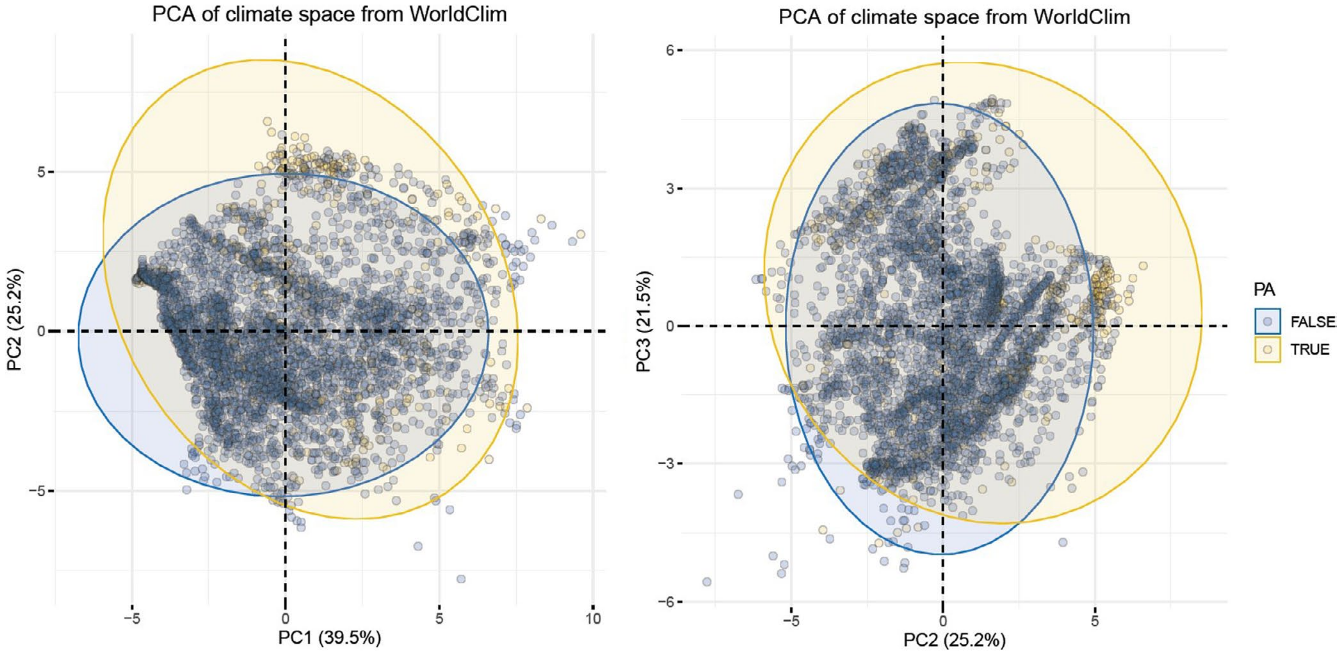

FIGURE 4 Principal components illustrating climate space captured by currently protected areas (yellow ellipses) relative to the climate space encompassed by South Africa (blue ellipses). Graph on the left shows the first two principal component axes (PC1 and PC2), explaining 39.5% and 25.2%, respectively, of the total variation, graph on the right shows the second and third principal component axes (PC2 and PC3), explaining 25.2% and 21.5%, respectively, of the total variation. Climate data extracted from the WorldClim database (Hijmans et al., 2005) (http://worldclim.org) used for fitting the species distribution models

irrespective of species migration capacity. It is likely that dispersal barriers and other non-modelled features will limit species' abilities to occupy the full extent of their suitable climate space. We suggest, therefore, that effective conservation requires a diversity of approaches, including the maintenance of the current protected area network, and the purchasing of small fragments of land where species find refugia, creating corridors along climate gradients to allow species to track their climate niche (Imbach et al., 2013) and actively involving landowners in stewardship programmes. In some instances, pro-active management in the form of assisted dispersal, translocation of species or planting of seedling in new areas may be necessary (Caplat et al., 2016; Chapman et al., 2012; Christmas et al., 2016; Gallagher et al., 2015; Renton et al., 2012; Rutherford et al., 1999).

5 | SUMMARY

We show that, under future climate projections, many species may benefit from a relative increase in the proportion of their projected range extent within conservation units, but frequently this is associated with projected range contraction outside protected areas, and some species will experience both range contraction and a loss of protected area coverage. Our results, using the threatened endemic flora of South Africa as a case study, illustrate the importance of integrating climate change into Red Listing and conservation planning. Although there remains uncertainty surrounding climate projections and on how closely species will track shifting climates, we believe it would be a serious error to use this as justification for inaction.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The species occurrence data set for the threatened endemic plants of South Africa and the GIS shapefile of protected areas within the country are available for download from the Knowledge Network for Biocomplexity (https://knb.ecoinformatics.org) at https://doi.org/10.5063/F1BZ64GD. The original datafile for the protected areas network is available from the Department of Environmental Affairs, South Africa at https://portal.environment.gov.za/DEADownloads/Default.aspx. Historical and projected climate data for fitting and projecting species current and future distributions are available directly from the Knowledge Network for Biocomplexity at: https://doi.org/10.5063/F1765CR0. These data were extracted from the WorldClim database (Hijmans et al., 2005) (http://worldclim.org). The 19 bioclimatic interpolated climate station records from 1950 to 2000 used to model current distributions can be downloaded here: https://www.worldclim.org/data/worldclim21.html. Future climate projections are available here: https://worldclim.org/data/v1.4/cmip5_10m.html.

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