



# Moving with your mutualist: Predicted climate-induced mismatch between Proteaceae species and their avian pollinators

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## Abstract

**Aim:** Climate change influences species distribution in space and time, but predicting the overlap in the range of interacting species under different climate scenarios remains a challenge. Here, we explore how climate change influences shifts in species ranges among mutualists.

**Location:** Cape Floristic Region (CFR), South Africa.

**Taxon:** Proteaceae and Passeriformes.

**Methods:** We used machine-learning algorithms (random forest and boosted-regression trees) and regression model (generalized additive models) to predict range shifts of 11 bird-pollinated Proteaceae species, combined occurrence prediction of 71 bird-pollinated Proteaceae and their two most important, endemic, pollinator bird species. We determined the degree of overlap in geographical ranges of nectar-feeding birds and Proteaceae under different climate scenarios. Species ranges were projected to the years 2050 and 2070 using representative concentration pathways (RCP) 4.5 and 8.5 and three global climate models.

**Results:** The majority of Proteaceae species in our model are predicted to experience range contractions, which ranged from 1% under 2050 RCP 4.5 CCSM4 to 79% under 2070 RCP 8.5 CNRM-CM5 climate scenarios, leading to 55% and 62% range loss for Cape sugarbird and orange-breasted sunbird, respectively, under extreme climate scenarios. Proteaceae species are predicted to experience least overlap with nectar-feeding birds in the northern and eastern range under future climate scenarios.

**Main Conclusion:** Climate change threatens species occupying the mountain range of the northern limit and other regions of the CFR. Reduced range overlap of mutualists may have significant implications for the reproduction and persistence of Proteaceae. We suggest active monitoring of Proteaceae populations in regions where species are predicted to lose their range, particularly so for threatened species with small ranges.

## KEYWORDS

mountain range, nectar-feeding birds, plant-pollinator interactions, range contraction, specialist pollinators, sugarbird, sunbird

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## 1 | INTRODUCTION

Climate shapes the range of species across latitudinal and elevation gradients (Zu et al., 2021), and this may cause local extirpation when the climate envelopes of species contract (Cahill et al., 2013). Climate change-induced extinction may influence the loss of more species or groups than originally predicted, as a result of intrinsic dependence among species (Schleuning et al., 2016). This is of particular importance for ecological interactions, where the loss of a mutualistic partner may lead to declines in ecosystem functions (Pyke et al., 2016) and species co-extinction (Sonne et al., 2022). Generally, species are expected to shift their ranges towards the poles or higher elevation (Freeman et al., 2018; Zu et al., 2021), but species' responses to climate are also mediated by dispersal traits, causing species to shift their ranges at different paces (Urban et al., 2012). This may result in a mismatch in the distribution range of mutualistic partners (Gómez-Ruiz & Lacher Jr, 2019) and lead to local extinction for species in highly specialized mutualistic interactions (Bascompte et al., 2019).

Pollinators are essential for reproduction of many plant species (Pauw, 2007; Stanley et al., 2020) and are often considered as important biotic factors mediating flowering plant species' distribution across environmental gradients (Johnson, 2010). Synchrony in phenology and distribution range of pollinator-dependent flowering plants and animal pollinators is required for effective pollination and the reproduction of flowering plants (Adedjoja et al., 2020; Hegland et al., 2009). Many pollinators and flowering plant species are predicted to shift their ranges in response to climate change; thus, mismatch in the range of pollinators and dependent flowering plants could occur, causing a reduced co-occurrence of plant and pollinators in shared habitats (Gérard et al., 2020; Schweiger et al., 2008). For flowering plants that depend solely on animal pollinators for sexual reproduction, this may lead to population declines.

In the Cape Floristic Region (CFR) of South Africa, nectar-feeding birds are important pollinators of flowering plants, especially for Proteaceae (Geerts, 2011). This dependence is highly asymmetric, with only six nectar-feeding bird species existing in this region, but approximately 70 species of Proteaceae, dependent on these nectar-feeding birds for reproduction (Geerts et al., 2020; Pauw & Johnson, 2018). Of the six nectar feeding birds in this region, four occur throughout, and of these, the Cape sugarbird *Promerops cafer* and orange-breasted sunbird *Anthobaphes violaceae* are endemic to this region. These two bird species, especially sugarbirds, are frequent visitors of Proteaceae (Botha, 2017; Schmid et al., 2015). Proteaceae form an integral biotic component of the fynbos biome of the CFR forming the canopy in mature fynbos biome (Vlok & Yeaton, 1999) and occurring extensively throughout the CFR. Most of the Proteaceae dominating the fynbos biome are endemic to this region and provide sugar-rich nectar, especially during the breeding season for nectar feeding birds (Geerts, 2011; Geerts et al., 2020). However, the distribution of these plant species is threatened by alien invasive species, too frequent fires, but also climate change.

Like other Mediterranean-type ecosystems, the climate of the CFR is changing due to the increase in temperatures and reduced

rainfall (Tyson et al., 2002). The CFR is predicted to experience an increase of 1.8°C in mean annual regional temperature by the year 2050 (Midgley et al., 2003), and a significant proportion of suitable habitat for Proteaceae species is predicted to be lost from the northern and eastern limits of this biome due to climate change (Midgley et al., 2002). Shifts in species' ranges are thus imminent and this may lead to mismatches in distribution among mutualistic partners. Several studies have assessed how drivers of biodiversity change, such as land use (Hauber et al., 2022; Mnisi et al., 2021), biological invasion (Adedjoja et al., 2021; Geerts & Adedjoja, 2021; Geerts & Pauw, 2009) and fire (Adedjoja et al., 2019; Geerts et al., 2012), lead to decline in the diversity and pollination rate of flowering plants, and Proteaceae in particular, in the fynbos biome. However, despite substantial evidence of the effect of climate change on species distribution, very few studies consider climate change-induced range shift in Africa (Kuhlmann et al., 2012; Lee & Barnard, 2015; Midgley et al., 2002, 2003; Simmons et al., 2004), and no study has considered how climate change may lead to a mismatch in the distribution of flowering plants and vertebrate pollinators in Africa. In fact, mismatch between plants and pollinators under climate change has rarely been studied globally (but see Gómez-Ruiz & Lacher Jr, 2019; Kolanowska et al., 2021).

Several studies have predicted species will experience significant shifts in current range under future climate conditions (Kuhlmann et al., 2012; Midgley et al., 2002; Zu et al., 2021), but predicting how the range shift of pollinators will track that of flowering plants is essential in identifying ecosystems where pollination ecosystem function is threatened. Here, we explore how climate change influences shifts in species ranges among mutualists in the CFR, we applied environmental niche modelling for each of 11 bird-pollinated Proteaceae species, for combined occurrences of 71 bird-pollinated Proteaceae and each of two important nectar-feeding bird pollinators which are endemic to this region. A previous study has predicted that the climate of the CFR, especially in the northern limit, will get drier and warmer in the future (Midgley et al., 2005); hence, we hypothesize that bird-pollinated Proteaceae and endemic nectar-feeding bird pollinators will experience range contraction in this region under future climate scenarios. We also hypothesize that the rate of range contractions will vary between Proteaceae and bird pollinators, leading to predicted changes in the degree of geographical range overlap of bird-pollinated Proteaceae and nectar-feeding birds under future climate scenarios.

## 2 | MATERIALS AND METHODS

### 2.1 | Data sources

We obtained Proteaceae distribution data from the Protea Atlas Project database. Approximately 242,200 species occurrences were recorded by volunteers in 58,362 plots across the region between 1991 and 2002 (Rebello, 2006). During this period, volunteers recorded the population of each Proteaceae species within the 500 m

diameter observation plots and species were classified as abundant (more than 10,000 records), common (101–10,000 records), frequent (10–100 records), rare (1–9 records) and extinct (known localities where plants were absent). For this study, we used only abundant, common and frequent observation records. Of the 330 Proteaceae species in the CFR, we selected only the bird-pollinated species (according to Geerts et al., 2020) which had more than 1200 presence observation records. Based on these criteria, we included 11 species: *Protea repens*, *P. laurifolia*, *P. lorifolia*, *P. cynaroides*, *P. eximia*, *P. neriifolia*, *P. nitida*, *P. lepidocarpodendron*, *Mimetes cucullatus*, *Leucospermum cuneiforme* and *L. conocarpodendron viridium*.

Of all the nectar-feeding birds in the entire CFR, we selected two species (Cape sugarbird *P. cafer* and orange-breasted sunbird *Anthobaphes violacea*), which are endemic to this region and known to frequent *Protea* stands. We obtained bird distribution data from the Southern Africa Bird Atlas Project 2 database (SABAP2). Data collection began in 2007 and data collected until 15 November 2021 were used in this study. Both SABAP2 and PAP databases contain records of presence and true absence, and species distribution data were clipped using the Cape boundary layer derived from the Cape Action for People and Environment project (CAPE). The distribution of several species is limited to this region as the Cape is bounded by ocean in the south, drier climate in the north and changing rainfall regime in the east. For SABAP2, species occurrence was recorded as checklists in grids with a pentad resolution of 5' × 5' (approximately 8 km by 8 km). The *Protea* Atlas Project, on the other hand, has high-resolution species occurrence records as points with geographic coordinates of 50–100 m accuracy. To convert the Proteaceae occurrence distribution data to the same resolution as nectar-feeding birds, we assigned a presence to every SABAP2 grid cell with at least one plant of the focal Proteaceae species. This was done for each of the 11 Proteaceae species. In addition to the selected Proteaceae species, we combined the occurrence record of all 71 bird-pollinated Proteaceae species in CFR (see Geerts et al., 2020 for full list of Proteaceae species) into one occurrence record specifying grid cells with at least one Proteaceae occurrence as '1' and grid cells with no Proteaceae as '0'. This indicates regions in the CFR where at least one bird-pollinated Proteaceae will occur in addition to the selected 11 individual Proteaceae species with the most abundant occurrence records in the PAP database.

## 2.2 | Environmental data

We extracted 19 bioclimatic variables, averaged between 1970 and 2000 from the WorldClim database (<https://www.worldclim.org>) at 5-minute resolution to match the resolution of bird and plant distribution data. Using the 'raster' package (Hijmans et al., 2015) in R, climate data were cropped to the limit of the Cape boundary to ensure outputs from our models are for the geographic range of the CFR only. To reduce multicollinearity among environmental variables (Dormann et al., 2013), we used the 'varclus' function of the 'Hmisc' package in R, to assess correlation among bioclimatic variables, and

only variables more directly affecting plant and bird physiology according to expert opinion were retained for our models when any two variables were above the threshold of  $|r| > 0.7$ . Finally, seven bioclimatic variables (Bio 1 'annual mean temperature', Bio 3 'isothermality', Bio 4 'temperature seasonality', Bio 6 'minimum temperature of coldest month', Bio 8 'mean temperature of wettest quarter', Bio 9 'mean temperature of driest quarter' and Bio 15 'precipitation seasonality') were selected and included in our model predictions for the selected 11 Proteaceae species and combined occurrences of 71 bird-pollinated Proteaceae.

Model predictions for nectar-feeding birds were computed using three different predictor groups. We included all seven bioclimatic variables as predictors to understand how climatic abiotic factors affect the range of nectar-feeding birds. Also, the nectar-feeding birds are highly dependent on Proteaceae as primary food source, and climate change will likely affect the distribution of nectar-feeding birds through the range contraction or expansion of Proteaceae in response to climate change. To assess how the changes in Proteaceae range affect the response of nectar-feeding birds to climate change, we also developed models with Proteaceae as predictors of bird occurrences. In these models, we included the occurrence probabilities of each 11 Proteaceae species together with the seven bioclimatic variables. In the third model, we included the combined occurrence probabilities of all 71 bird-pollinated Proteaceae with the seven bioclimatic variables as predictors to account for the broader feeding niche of the birds and how they influence the response of nectar-feeding birds to climate change. We applied Pearson's correlation coefficient to estimate the similarity between models including bioclimatic variables only and models including bioclimatic variables with the 11 individual Proteaceae species occurrence, as well as models including bioclimatic variables with the combined 71 bird-pollinated Proteaceae occurrence.

For future projections, climate scenarios for the years 2050 and 2070 were derived from the CCSM4, CNRM-CM5 and MIROC global climate models (GCM). Data were extracted following the previously described protocol under two different Intergovernmental Panel on Climate Change conditions for the representative concentration pathways (RCP) class: RCP 4.5 (mild scenario of CO<sub>2</sub> emission and temperature rise of 2°C by 2100) and RCPs 8.5 (extreme scenario of CO<sub>2</sub> emission and temperature increase of 5°C by 2100).

## 2.3 | Environmental niche modelling

The current and future distribution of nectar-feeding birds and selected Proteaceae species were modelled using three approaches: random forest (RF), boosted regression tree (BRT) and generalized additive modelling. RF and BRTs are both machine-learning techniques that ensemble classification and regression trees using bagging or boosting for RF models (Strobl et al., 2009) and BRTs (Valavi et al., 2021), respectively. Generalized additive models (GAM) is a regression technique that applies smooth functions to assess the effect of predictors on response variables. Compared

to other species distribution modelling (SDM) algorithms, machine learning algorithms are suitable for predicting complex relationships (Ramampandra et al., 2023) with RF and BRT known to provide high prediction performances, while GAM is a highly flexible regression approach suitable for modelling data that do not require interactive terms (Elith et al., 2006). RF was applied using the 'randomforest' R package (Liaw & Wiener, 2002), BRT using the 'gbm' R package (Greenwell et al., 2019) and GAM using the 'mgcv' R package (Wood, 2017). The three modelling algorithms were combined into an ensemble model using the mean of the three models to reduce the uncertainty of individual model predictions (Dormann et al., 2018).

Model performance was estimated using spatial cross-validation, which accounts for spatial autocorrelation by splitting occurrence records into spatial clusters as described by Ploton et al. (2020). Spatial correlation was determined using empirical variogram (Figure S1) and correlogram of Moran I (Figure S2) for each species. The empirical variogram revealed varying spatial correlation up to approximately 70–100 km for each species (Figure S1). Occurrence records of each species were divided into 33 equal area clusters within the CFR area using the maximum range of spatial autocorrelation (105 km, a slightly longer distance than range of autocorrelation (Ploton et al., 2020)) as the distance between pixels in clusters for all species and we ran spatial clusters in 10-fold using all but onefold per fitting round. The area under curve (AUC) of receiver operating characteristic (ROC) and True Skill Statistics (TSS) were used as a measure of model evaluation. Models with AUC values >0.7 and TSS >0.4 are considered good and retained.

## 2.4 | Species range change and overlap between pollinator and plant species

To quantify the overall percentage range size of each Proteaceae species, the combined 71 bird-pollinated Proteaceae and each nectar-feeding bird species, we divided the sum of all occurrence probabilities per cell by the number of all cells for each species under different climate scenarios. In addition, we quantified the proportion of loss or gain in species' suitable habitat under current and future climate conditions by estimating the percentage difference in the overall current and future range size for each species under different climate scenarios.

To determine the proportion of overlap in the geographical range of nectar-feeding birds and Proteaceae, we compared the predictions of each species of Proteaceae with each species of nectar-feeding birds using the Warren I index (Warren et al., 2008) which estimates similarity in geographical space overlap of two distributions. Warren I index ranges from 0 to 1, with '0' indicating no overlap and '1' indicating complete overlap of two predicted distributions. To understand how species' geographical range overlap varies among climate scenarios, we estimate changes in Warren I index overlap for each comparison of geographical range of bird and plant

across time periods (year and RCPs) using Kruskal–Wallis test. To determine regions where overlap or mismatch will occur between the range of nectar-feeding birds and the combined 71 bird-pollinated Proteaceae under current and future climate scenarios in the CFR, we transformed species' occurrence probabilities into presence/absence maps using the threshold that maximizes TSS (Liu et al., 2016). All analyses were conducted in R 4.2.2 (R Core Team, 2022), and maps were plotted in QGIS 3.20.

## 3 | RESULTS

All predictions revealed high performance as indicated by a cross-validation AUC >0.7 for each Proteaceae and nectar-feeding bird species, and combined projection of all bird-pollinated Proteaceae (Table S1). Although all predictions revealed high performance, Random-Forest predictions and ensemble models show higher AUC values compared to GAM predictions for all Proteaceae species except *Protea eximia* (Table S1).

### 3.1 | Plant predictions

Habitat suitability for each Proteaceae species in our model is predicted to decrease under all climate scenarios and time periods (Figure 1; Table S2) except for *L. conocarpodendron*. The average decline in suitable habitat of each Proteaceae and the combined projection of the 71 bird-pollinated Proteaceae was approximately 47.36% under the MIROC climate scenario, and 45.61% and 39.19% under the CNRM-CM5 and CCSM4 climate scenarios, respectively. Across projected time periods, predicted average decline in the year 2070 in suitable habitat was 52.50% and 44.84% under RCPs 8.5 and 4.5, respectively. In the year 2050, predicted average decline in suitable habitat was 41.74% and 37.11% under RCPs 8.5 and 4.5, respectively.

Our predictions show considerable variation in each Proteaceae species' response to different climate scenarios and time periods (Figure 1). *Protea laurifolia* is predicted to suffer the greatest loss of suitable habitat of 78.80% under the extreme 2070 RCP 8.5 CNRM-CM5 climate scenario (Figure 1; Table S2). Other Proteaceae species, especially *P. repens* and *P. nitida*, which currently occupy the largest range with 34.40% and 26.57%, respectively, are predicted to suffer >50% loss of suitable habitat under the extreme 2070 RCP 8.5 climate scenarios for all GCMs (Figure 1; Table S2). *Protea lepidocarpodendron* currently occupies 1.75% of the CFR, the smallest range among all modelled Proteaceae, but this species is also predicted to lose >50% of suitable habitat under the extreme 2070 RCP 8.5 for all GCMs (Figure 1; Table S2). Among all modelled Proteaceae species, the genus *Leucospermum* is predicted to experience the lowest range change, especially under mild climate scenarios where *L. conocarpodendron* is predicted to experience a 24.40% gain in suitable habitat (Table S2). When we compiled the occurrence probabilities

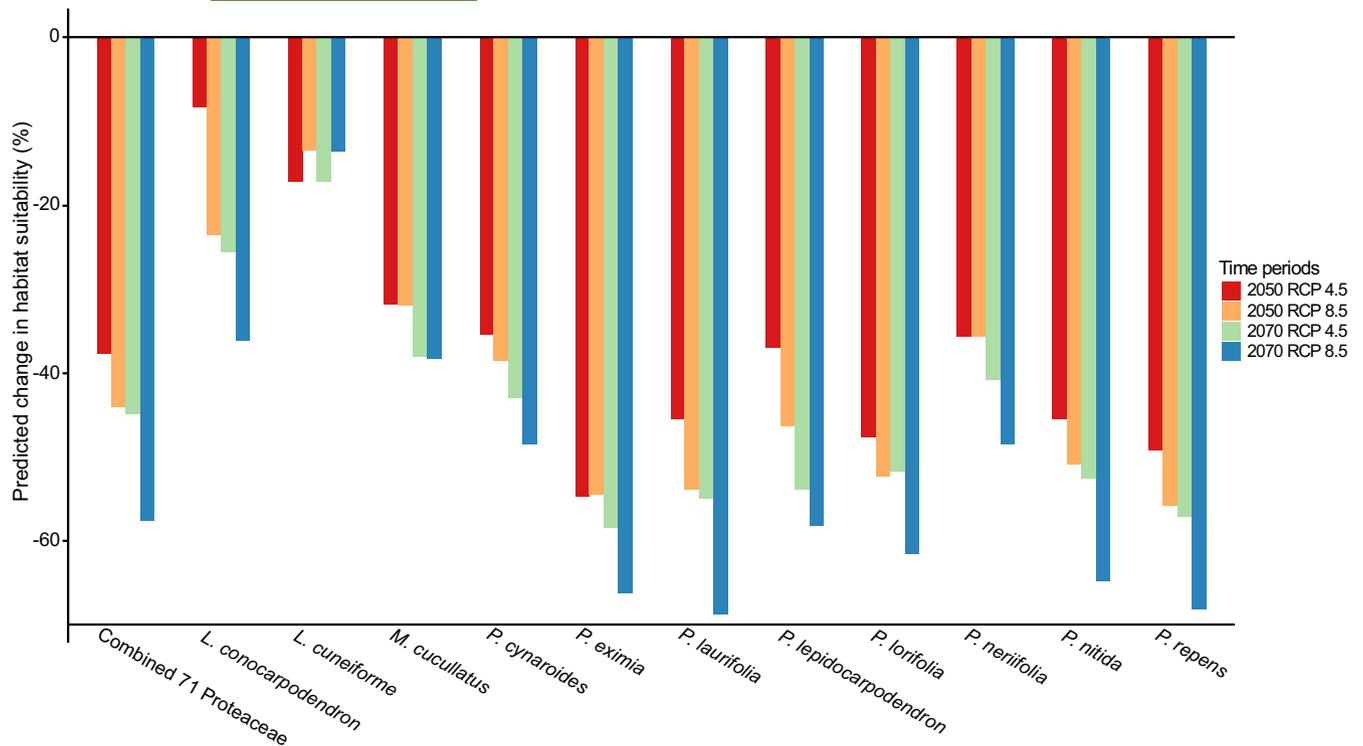


FIGURE 1 Percentage change in habitat suitability of each Proteaceae species and the combined occurrence of 71 bird-pollinated Proteaceae at different time periods averaged across three GCMs. GCM, global climate models.

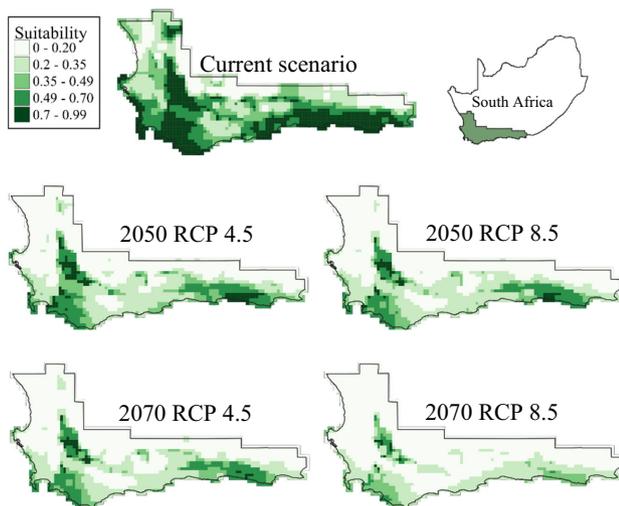


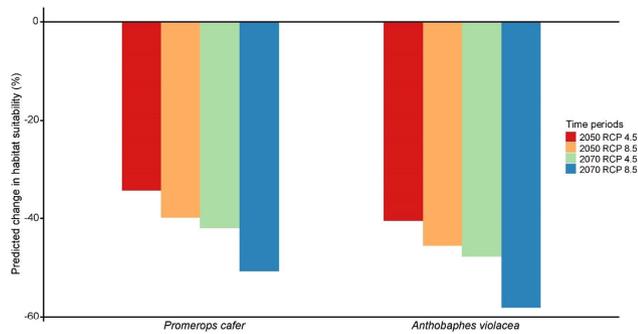
FIGURE 2 Projected occurrence probabilities of the combined 71 bird-pollinated Proteaceae predicted by SDM model with climate variables as predictors across different time periods (RCPs and years) averaged across three GCMs. Map of South Africa is included showing the coverage of the Cape Floristic Region. GCM, global climate models; RCP, representative concentration pathways; SDM, species distribution modelling.

of all 71 bird-pollinated Proteaceae, the probability of occurrence of at least one Proteaceae decreased by approximately 60.79% under the extreme 2070 RCP 8.5 CNMR climate scenario (Figure 1; Table S2), especially in the northern and eastern limit of the biome (Figure 2).

### 3.2 | Bird predictions

Model performance for the prediction of *P. cafer* and *A. violacea* was consistent across all predictor categories (abiotic climatic variables only, 11 modelled Proteaceae prediction with climatic variables and combined 71 bird-pollinated Proteaceae prediction with climatic variables) with approximate AUC values of 0.84 and 0.83 and TSS values of 0.55 and 0.52 for *P. cafer* and *A. violacea*, respectively (Table S1). The predictions from all models with different predictors were highly correlated for *P. cafer* (climate only vs. climate with individual 11 Proteaceae prediction  $0.904 < r < 0.951$ ; climate only vs. climate with combined 71 bird-pollinated Proteaceae prediction  $0.993 < r < 0.997$ ) and *A. violacea* (climate only vs. climate with individual 11 Proteaceae prediction  $0.891 < r < 0.952$ ; climate only vs. climate with combined 71 bird-pollinated Proteaceae prediction  $0.978 < r < 0.993$ ) (Table S3).

We selected models using climate with 11 Proteaceae as predictors for the projections of nectar-feeding birds since these models show lower correlation with climate only models compared to models including climate with all 71 Proteaceae. Both nectar-feeding birds are predicted to suffer significant loss in suitable habitat across all climate scenarios (Figure 3; Table S2). The lowest losses of approximately 28% and 34% in suitable habitats of *P. cafer* and *A. violacea*, respectively, are predicted to occur under the mild 2050 RCP 4.5 CCSM4 climate scenario. *Promerops cafer* is predicted to experience the greatest loss of approximately 55% in suitable habitat under the extreme 2070 RCP 8.5 MIROC scenario, while *A. violacea* is predicted to experience the greatest loss of 61.53% of suitable



**FIGURE 3** Percentage change in habitat suitability of nectar-feeding birds under different time period averaged across three GCMs. GCM, global climate models.

habitat under the extreme 2070 RCP 8.5 CNRM-CM5 climate scenario (Figure 3; Table S1). Both nectar-feeding bird species are predicted to lose most of their range in the northern and eastern limit of the biome (Figure 4), and considerable portion of the extreme western limit for *A. violacea* (Figure 4b).

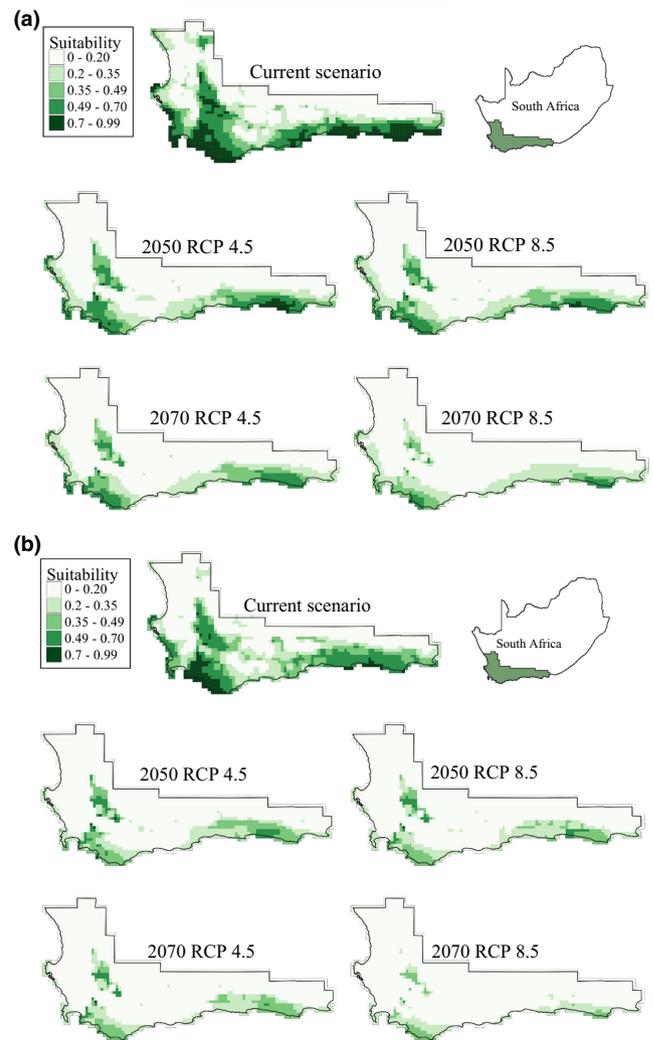
### 3.3 | Overlap in geographical range of Proteaceae and nectar-feeding birds

Our predictions reveal considerable variation in the current geographical range overlap of different Proteaceae species and nectar-feeding birds. *Protea lepidocarpodendron* and *L. conocarpodendron* show lowest average overlap in geographical range with *P. cafer* (Warren I=0.69) and *A. violacea* (Warren I=0.67), while *P. repens* and *P. cynaroides* are predicted to have the highest average overlap in geographical range with *P. cafer* (Warren I=0.96) and *A. violacea* (Warren I=0.97) (Table S4). Individual Proteaceae species in our models show consistent degree of geographical space overlap with *A. violacea* across all time periods. Majority of the Proteaceae species show consistent degree of geographical range overlap with *P. cafer* across all time periods. However, there was a significant difference in the geographical range overlap of *P. cafer* with *L. conocarpodendron* (Kruskal–Wallis chi-square=7.67, df=3, p=0.053, Figure 5) and *P. lepidocarpodendron* (Kruskal–Wallis chi-square=7.89, df=3, p=0.048, Figure 5) across time periods. The highest overlap of *P. cafer* with these two Proteaceae species is predicted to occur under the extreme 2070 RCP 8.5.

The prediction of combined 71 bird-pollinated Proteaceae shows consistent degree of overlap with *A. violacea* and *P. cafer* across time periods. Range overlap map reveals that the predicted range of Proteaceae will contract to areas mostly suitable for nectar-feeding birds under future climate scenarios (Figure 6).

## 4 | DISCUSSION

Climate change, to a large extent, can determine the relationship between animal pollinators and dependent flowering plants in space



**FIGURE 4** Projected occurrence probabilities of (a) *Promerops cafer* and (b) *Anthobaphes violacea* predicted by SDM model with climate and 11 Proteaceae as predictors across different time periods (RCPs and years) averaged across three GCMs. Map of South Africa is included showing the coverage of the Cape Floristic Region. GCM, global climate models; RCP, representative concentration pathways; SDM, species distribution modelling.

and time. Our models reveal a significant decline in suitable habitat of nectar-feeding birds and majority of Proteaceae species under all future climate scenarios. Most of the species included in our model are predicted to suffer the greatest decline in suitable habitat under the extreme 2070 RCP 8.5, especially in the northern limits of the biome. Although bird pollinators are predicted to lose range in the future as Proteaceae species range contracts, bird pollinators show fairly consistent range of overlap with bird-pollinated Proteaceae across different time periods, with the exception of *L. conocarpodendron* and *P. lepidocarpodendron* which are predicted to share most of the range of nectar-feeding birds under extreme climate scenarios. Climate change may shrink the range of nectar-feeding birds, especially in the northern limit where a significant proportion of the range of Proteaceae will be lost, restricting suitable habitat for nectar-feeding birds only to regions where Proteaceae species are predicted to occur.

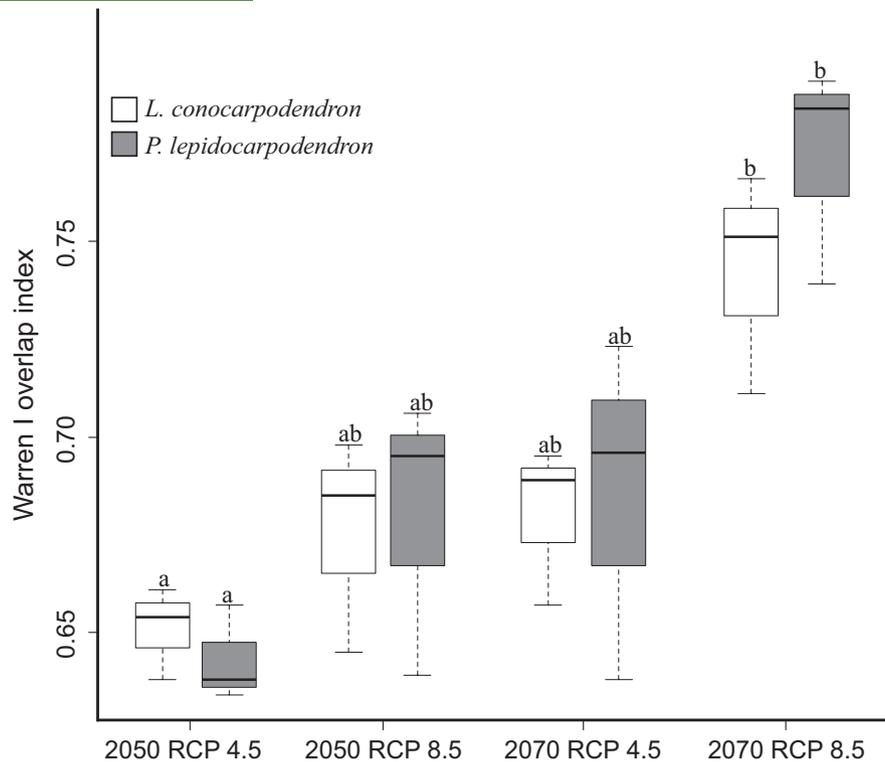


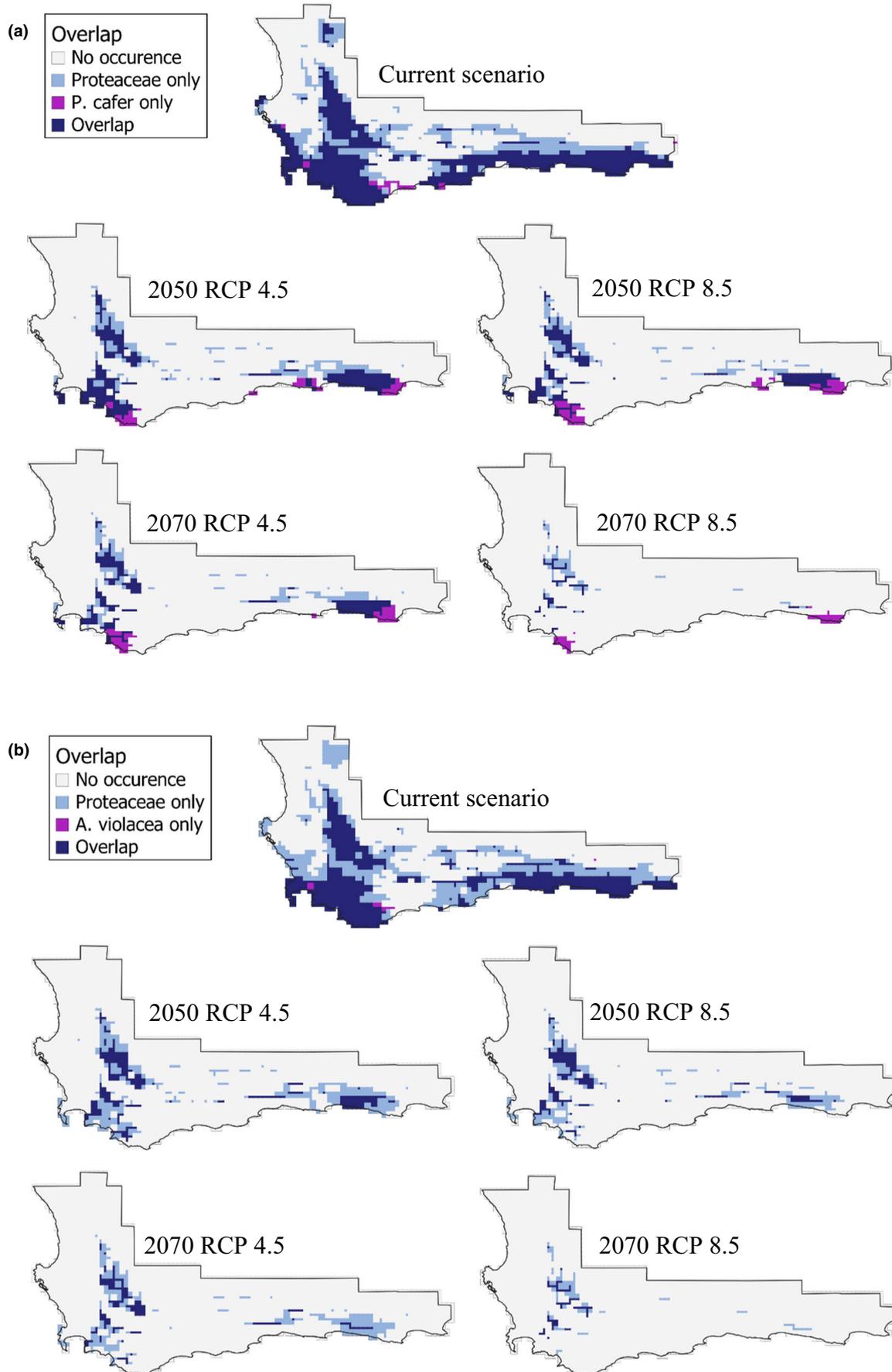
FIGURE 5 Warren I index showing the degree of geographical range overlap of *Promerops cafer* with *Leucospermum conocarpodendron* and *Protea lepidocarpodendron* across time periods. Different letters show significant differences among time periods at  $\alpha=0.05$  for each Proteaceae species.

In this study, the probabilities of occurrence of Proteaceae species and nectar-feeding birds are driven by bioclimatic variables associated with varying level of greenhouse gas concentrations. Generally, higher greenhouse gas concentrations RCP 8.5 under all climate models indicated largest decline in suitable habitats of Proteaceae and nectar-feeding birds, especially in the year 2070. One of the most striking pieces of evidence of climate change in South Africa is the increased warming of the winter rainfall area, especially the CFR (Warburton et al., 2005), leading to the predicted loss of important species in this region (Midgley et al., 2002; Rutherford et al., 1999). The ranges of *P. cafer* and *A. violacea* have declined by 15% and 13%, respectively, in the past two decades, partly due to inability of these birds to adjust their physiological response to increased warming (Lee & Barnard, 2015). In this study, these bird species are predicted to lose approximately 55% and 61% of their range, respectively, under the extreme 2070 RCP 8.5 MIROC and CNRM-CM5 scenarios. Bird pollinators in South Africa, especially our study species with ranges restricted to the CFR, are at the greatest risk of population decline due to climate change, as they may be unable to adapt to new suitable environment under future climate conditions (Simmons et al., 2004). The climate projection of the CFR shows the region will get warmer and drier, leading to extreme events such as drought and wildfire (Hewitson & Crane, 2006; Midgley et al., 2005). For Proteaceae, which are sensitive to temperature and precipitation change, climate change may inhibit seedling germination or increase seedling mortality and the development of resprouting Proteaceae in this region (Mustart et al., 2012), as

temperature above species thermal range will induce poor development and decline in Proteaceae diversity (Louw et al., 2015).

Most of the Proteaceae species in our models are expected to suffer significant loss in suitable habitat, especially in the northern limit of the biome, which is similar to previous studies (Midgley et al., 2002, 2003). In the fynbos ecosystem, diverse bird-pollinated Proteaceae communities attract higher bird abundance and species richness, perhaps due to the sequential flowering of different Proteaceae genera which produce resources all year round (Geerts et al., 2020). As species' ranges contract, Proteaceae communities are likely to become less diverse and thus less likely to support bird populations. According to our model, *Protea lepidocarpodendron*, *P. laurifolia*, *P. nitida*, *P. repens*, *P. eximia* and *P. lorifolia* appear to be the most affected by extreme climate conditions, as they are predicted to suffer at least 50% loss of suitable habitat consistently under each climate model in the year 2070. *Protea lepidocarpodendron*, a near-threatened species (Rebelo et al., 2020), grows only in sandstone, ferricrete and granite soils (Rebelo, 2001). This species, which is predicted to lose approximately 61% of its range under 2070 RCP 8.5 MIROC climate scenario, currently occupies the smallest range among all Proteaceae in our model and may be unable to shift its range under future climate conditions.

Our models predicted varying degree of overlap in geographical range of nectar-feeding birds and Proteaceae, with some widely spread Proteaceae, such as *P. repens* and *P. cynaroides*, showing higher degree of geographical range overlap with nectar-feeding birds. Nectar-feeding birds are highly reliant on



**FIGURE 6** Range overlap maps of (a) *Promerops cafer* and all 71 bird-pollinated Proteaceae, and (b) *Anthobaphes violacea* and combined 71 bird-pollinated Proteaceae across different time periods (RCPs and years) averaged across three GCMs. GCM, global climate models; RCP, representative concentration pathways.

Proteaceae for adequate nectar, and these birds will track the geographical range of Proteaceae since food availability is an important determinant of species' habitat suitability (Kwit et al., 2004). Also, some Proteaceae, especially *P. lepidocarpodendron* and *L. conocarpodendron*, show varying degree of overlap with nectar-feeding birds across time periods, with highest overlap predicted to occur under extreme climate scenarios. *P. lepidocarpodendron* is rare and only occurs in the extreme western part of the biome, and *L. conocarpodendron* occupies the eastern range where nectar-feeding birds, especially *A. violaceae* are less represented. Under extreme scenarios, the suitable habitats for these Proteaceae will contract considerably to regions also predicted as partly suitable habitats for *P. cafer*, especially in the eastern range. *Anthobaphes violaceae* will lose considerable habitats in this region, and this may explain why the degree of overlap of *A. violaceae* with all Proteaceae remained consistent across time periods. Although *P. lepidocarpodendron* and *L. conocarpodendron* show greater overlap with nectar-feeding birds under extreme scenarios, they also demonstrate the lowest degree of overlap with nectar-feeding birds compared to other Proteaceae since they occur in a region where nectar-feeding birds, especially *A. violaceae*, will experience range contraction. If these species rely primarily on nectar-feeding birds as pollen vectors, they may experience significant decline in pollination success due to the low suitability of the habitat of these plants for bird pollinators, especially *A. violaceae*.

Our model prediction for the combined occurrence of 71 bird-pollinated Proteaceae shows contraction across majority of species range, especially in the northern limit, with most suitable habitats restricted to some part of the central range, and the southern tip of the eastern range under extreme climate scenarios. While *P. cafer* shows the tendency to occur in most parts of this range and is expected to track plant occurrence under different climate scenarios, suitable habitat for *A. violaceae* is predicted to be largely reduced, especially in the eastern and extreme western part of the biome. Furthermore, the reduction in ranges is likely to create disjunct populations, separating the western and eastern populations. Although birds and seeds may disperse across these gaps, intensified anthropogenic land transformation can limit or prevent this dispersal. This may limit pollination success for many bird-pollinated Proteaceae, especially species highly reliant on *A. violaceae* for pollination under extreme climate scenarios.

Climate change influences species diversity and distribution through several complex pathways, but factors such as population dynamics, dispersal ability, ecological interactions, genetic composition and availability of food sources can influence the species response to climate change (Clarke, 1996). Mutual dependence of pollinators and flowering plants can cause species coextinction, especially in highly specialized interactions. The coexistence of nectar-feeding bird pollinators and Proteaceae in a highly asymmetrical ecological interaction (Geerts et al., 2020) leads us to expect asymmetrical responses to climate change. Although nectar-feeding birds are predicted to lose suitable habitats in some areas suitable for Proteaceae species under future climate conditions, this is

more evident for the *A. violaceae* than *P. cafer*. In the CFR, the bird-pollinated Proteaceae are primarily pollinated by four bird species; thus, declining diversity of bird pollinators may lead to cascading losses of dependent Proteaceae species, although this is yet to be determined. However, sunbirds forage from many Proteaceae species, as well as Ericaceae and geophytes in the CFR which receive visitation from sunbirds (Geerts et al., 2020; Schmid et al., 2015). The wide distribution of Proteaceae species and generalized foraging of nectar-feeding birds in this region enable the latter to switch its diet to the available Proteaceae species, for example, foraging on widely distributed *P. repens* in the absence of the rare *P. lepidocarpodendron*. Since reduced visitation by suitable pollinators can lead to reduced fitness of flowering plants (Pauw, 2007), bird-pollinated Proteaceae may be more susceptible to the impact of climate change compared to nectar-feeding bird pollinators (Bond, 1994). However, to fully understand how range mismatch translates into reduced reproduction and fitness of Proteaceae, long-term manipulative studies of species population in this region are required.

The CFR is characterized by complex topography, especially in the northern and eastern limits, and the rugged mountains of this region support high species endemism and diversity (Midgley et al., 2002). According to our model, nectar-feeding birds and Proteaceae appear to be losing suitable range in these areas of complex topography at the northern and eastern limits of the biome. This implies most mountain-dwelling Proteaceae will likely lose suitable range under future climate conditions. Usually, species occupying mountain ranges are predicted to move to areas of cooler temperatures at higher altitudes (La Sorte & Jetz, 2010; Zu et al., 2021). Most species living in the mountains often experience range contractions due to limited dispersal range, since high-elevation dwellers often lack other higher elevations to accommodate them when they reach the summit (Sekercioglu et al., 2008). Freeman et al. (2018) showed shrinking range sizes for birds occupying higher elevations, resulting in declining abundance and loss of some common species in the Peruvian mountain. As far as we know, there is no published information on how nectar-feeding birds and Proteaceae occupying the topographically diverse range of the northern and eastern limit of the CFR will shift their range across altitudinal gradients in response to climate change, but we expect range contractions for most species in this region. This may drive the extirpation of some important high-elevation Proteaceae from this region.

## 5 | CONCLUSION

Climate change continues to threaten biodiversity, and this is highly significant for species occupying the mountain range of the northern limit of the CFR. The mountain range is often the border for species range shift, and species loss at mountain limits illustrates the widespread projections that climate change will influence the extinction of approximately 10% of all living organism by 2100 (Thomas et al., 2004). Although some species experiencing range loss in the northern limit of this region will likely experience range shifts or range

dislocation to the southern limits (Midgley et al., 2002). Nectar-feeding birds track the range contraction of most Proteaceae in our model, but some Proteaceae will also occur outside suitable geographical range of nectar-feeding birds, especially *A. violaceae* under future climate scenarios, and this may have a significant implication for the reproduction and persistence of Proteaceae in a new range. Although our ensemble model showed that Proteaceae range will contract largely due to changing climate, the extent of range loss of Proteaceae due to changing interspecific interactions with bird pollinators, which is difficult to determine, is unknown. Such data will be highly effective in making more accurate predictions of how future Proteaceae distribution is affected by biotic factors. We recommend active monitoring of the interspecific interactions and population dynamics of Proteaceae and nectar-feeding birds, especially in the northern and eastern limits of this region and also for some highly threatened species with limited distribution, such as *P. lepidocarpodendron*. Also, we recommend future studies to take into account dispersal ability of these species in order to fully understand how other specific traits contribute to species' responses to climate change and its associated range shifts.

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#### CONFLICT OF INTEREST STATEMENT

None.

#### DATA AVAILABILITY STATEMENT

All data analysed in this article are publicly available. The data that support the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.crjdfn37c>. The bioclimatic variables were obtained from Worldclim database (<https://worldclim.org/data/worldclim21.html>). Nectar-feeding bird occurrence data were obtained from the Southern Africa Bird Atlas Project (SABAP2) database (<https://sabap2.birdmap.africa/>), and the occurrence data for Proteaceae species were obtained from Protea Atlas Project database (<https://www.proteaatlas.org.za/>).

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## BIOSKETCH

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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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