








Niche dynamics modulate population connectivity between disjunct ranges of the Cape Robin-chat (*Cossypha caffra*) supporting an aridlands species pump

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Abstract

Southern Africa boasts an extraordinary diversity of birds, posited to have at least in part been driven by a “species pump” model, facilitated by an intermittent arid corridor connecting it with northeast Africa. This arid corridor arose and disappeared in concert with Plio-Pleistocene climate fluctuations, providing a means for northern, primarily arid-adapted lineages, to disperse to and subsequently colonize Southern Africa. Here, we test this “species pump” at the intra-specific level. We focus on Cape Robin-chats (*Cossypha caffra*) which have disjunct resident populations in the forested mountains of East Africa and in the aridlands of Southern Africa. We use multi-locus data to estimate gene flow between these populations, model spatial connectivity across this region contemporaneously and over the past 120 thousand years, and test niche differentiation. We found evidence for highly asymmetric gene flow (north to south) among Cape Robin-chat populations, and niche differentiation coupled with an inferred niche-based environmental filter limiting gene flow from southern to northern populations. Habitat suitability supports the presence of an intermittent corridor stretching from the Horn of Africa to Southern Africa. We propose that a modified species pump incorporating niche divergence and subsequent dispersal limitation driven by environmental filters has contributed to population differentiation among northern and southern populations of Cape Robin-chats, and that this same mechanism over time may have contributed to the rich avifaunal diversity of Southern Africa.

Highlights

- Southern Africa has rich avifauna with high endemism driven in part by *in situ* speciation.
- Using a combination of genetic analyses, niche models, and dispersal models, we find support for an intermittent aridlands corridor between disjunct populations of Cape Robin-chats modulated by Plio-Pleistocene climatic oscillations.
- This study shows niche divergence and asymmetric gene flow between southern and northern populations, providing a mechanism for population divergence.
- This supports the existence of an aridlands species pump that drives population divergence and may have contributed to species diversification in the Southern Africa avifauna.

Keywords

Africa, aridlands, biogeography, birds, disjunct range, niche overlap, population connectivity

Introduction

Latitudinal and elevational gradients are known to structure diversity across most terrestrial realms (Hillebrand 2004; Mittelbach et al. 2007; McCain and Grytnes 2010;

Smith et al. 2017; Dillon and Conway 2021). Species distributed across large latitudinal or elevational gradients experience associated environmental gradients. There are multiple means by which organisms can persist across disparate habitats and environments: they can have wide niche breadth (generalist species: (Slatyer et al. 2013; Carscadden et al. 2020)), occupy different portions of their fundamental niche space in different environments (plasticity: (Merila and Hendry 2014; Valladares et al. 2014)), experience niche evolution and local adaptation (Davis and Shaw 2001), or maintain the same niche, which along an environmental gradient might mean moving up or down slope, or north or south to track suitable climate (Parmesan and Yohe 2003; Moritz et al. 2008; Tingley et al. 2009).

Across Africa, these gradients play out across a highly dynamic landscape that has seen vast contraction and reorganization of forest habitats, and expansion of aridlands, dating to the Miocene (Zachos et al. 2001). A substantial body of work has focused on forest dynamics as drivers of diversification, as they relate to both forest-adapted (Bowie et al. 2006; Voelker et al. 2010; Portik et al. 2017; Leaché et al. 2019; Bowie et al. 2023) and aridland-adapted species (Lorenzen et al. 2012; Barlow et al. 2013; Voelker et al. 2016; Fuchs et al. 2017). There are multiple hypotheses to explain the origins of diversification and the disjunct distributions of Africa's aridland flora and fauna (Jürgens 1997; Kissling et al. 2016). One hypothesis posits that there was an intermittent aridlands corridor that connected northern and southern Africa, which stretched from the Horn of Africa in the northeast to south-western Africa (Balinsky 1962; Werger 1978). This corridor was identified based on the similarities of faunas between these regions (Balinsky 1962; Poynton 1995), and is of particular importance for southern African avian diversity. This corridor forms the basis of the "species pump" hypothesis, which posits that much of the regional southern African avian diversity arose when species adapted to drier xeric habitats colonized southern Africa during the Plio-Pleistocene climatic fluctuations (Voelker 2002; Voelker et al. 2012). This interchange is thought to have been driven by the periodic retraction of the Afrotropical forest and the establishment of the East African Savanna biome, allowing contact between northern and southern aridland areas and lineages (Fuchs et al. 2011; Lorenzen et al. 2012). Concordant with this hypothesis are several bird species that exhibit deep genetic structure between northern and southern aridland regions (Fuchs et al. 2011; Fuchs et al. 2017), and which have biogeographic reconstructions that support north to south movement through the corridor (Voelker 1999; Outlaw et al. 2007; Guillaumet et al. 2008). There are of course some exceptions that support a south to north movement, although fewer species fall into this pattern (Voelker et al. 2014; Voelker et al. 2016).

However, not all African bird species fit into the neat categorization of "aridland" or "forest" adapted species. The polytypic Cape Robin-Chat (*Cossypha caffra*) is widely distributed across the aridlands of southern Africa, and recent work has demonstrated that there are three genetic clusters in southern Africa that correspond with several

Pleistocene aridland habitat refugia (Wogan et al. 2020). In this part of its range, the Cape Robin-Chat can be found from sea-level up to 3000 m elevation on the South African escarpment, and is a generalist resident species that inhabits forest edges and parks, although is largely absent from forests (Hockey et al. 2005). It is found across most of the South African aridland habitats, and has within the past several hundred years colonized the extremely arid Nama Karoo Biome, from which it had been historically absent (Wogan et al. 2020). In addition to the Southern African populations, *Cossypha caffra* also has a disjunct range in Malawi, Tanzania, Kenya, Uganda, Rwanda, Burundi, and the Democratic Republic of Congo, and in this part of its range this species is a resident restricted to montane forest habitat, often along forest edges between 1500–3400 m (Hockey et al. 2005) (Fig. 1).

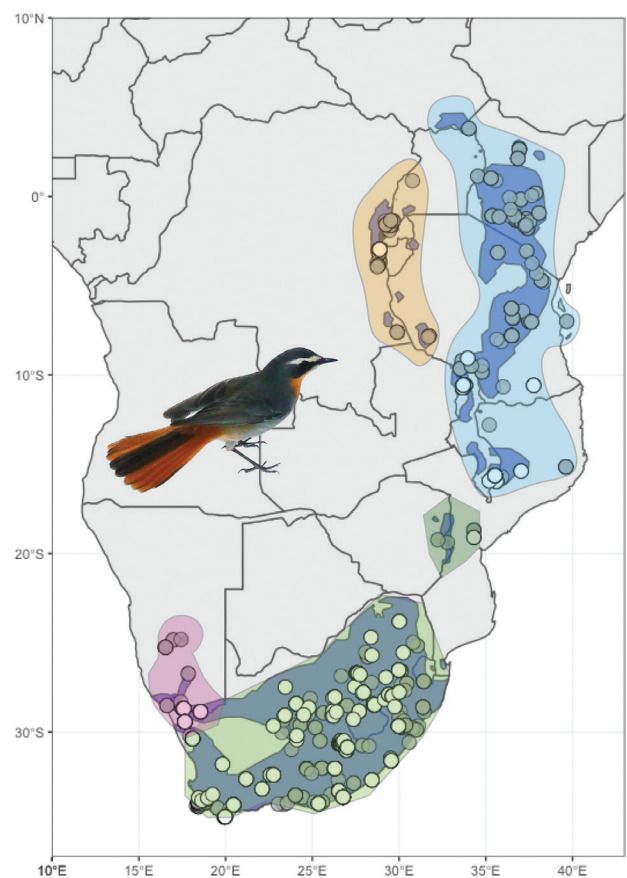


Figure 1. Geographic range of *Cossypha caffra*, by subspecies: *Cossypha caffra caffra* (green), *Cossypha caffra iolaema* (blue), *Cossypha caffra kivuensis* (orange), *Cossypha caffra namaquensis* (purple). In each colored-shaded area, the darker colored shape(s) reflect *Cossypha caffra* ranges denoted in Birdlife International, while the lighter colored shape is an expanded area to encompass samples from outside Birdlife's depiction of range. Within the expanded area, lighter circles are the sampling localities for which we generated genetic data, and darker circles are vouchered localities used for building ENMs obtained from our fieldwork and GBIF. Cape Robin-Chat by JMK - Own work, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=40318949>.

The diversity of habitats occupied in the northern and southern portions of the range, and the associated latitudinal gradient suggest that the northern and southern populations of *C. caffra* may be locally adapted to divergent environments. The shift to a new habitat may or may not be accompanied by an associated shift in the climatic niche of *C. caffra*. Since temperature, latitude and elevation are all tightly linked, for example with higher temperatures at both lower latitudes and lower elevations, from first principles we can expect that temperatures on tropical mountains and temperatures at high latitudes have the potential to be equivalent. For example, we know that a 100 meter increase in elevation causes a temperature decrease of up to $\sim 1^\circ\text{C}$, and is roughly equivalent to a latitudinal movement of ~ 197 km of distance in the southern hemisphere, since with each degree of increasing southern latitude, temperature decreases 0.5°C (La Sorte et al. 2014). Thus, the northern and southern populations, which span a latitudinal distance of over 35 degrees and an elevational gradient of over 3000 m, may each be adapted to substantially different climatic environments.

We hypothesize that the Plio-Pleistocene climatic oscillations created temporally dynamic corridors and barriers to population connectivity between the Horn of Africa and southern Africa. These dynamic corridors and barriers are respectively regions of high or low environmental suitability determined in part by the species niche. Niche dynamics are modulated by the extent of gene flow between populations since gene flow can either disrupt local adaptation by homogenizing the gene pool, or promote adaptation by increasing genetic variation and introducing advantageous alleles (Yeaman and Otto 2011; Savolainen et al. 2013; Tigano and Friesen 2016).

To determine the extent to which fluctuating corridors and niche dynamics may have played a role in structuring *C. caffra* populations, we estimate contemporary and historical population connectivity using a combination of environmental niche models and multi-locus genetic data. If population connectivity is low, gene flow between northern and southern populations will be reduced to absent and this would translate to substantial population structure and rare instances of admixed individuals with north and south parentage. Conversely, if population connectivity is high, gene flow will be extensive between northern and southern populations, which would result in little population substructure between northern and southern populations, and a high proportion of individuals with admixed parentage.

We also assess evidence for climatic niche conservatism or niche divergence accompanying the shift in habitat usage between the northern and southern populations of *C. caffra*. If the climatic niche is conserved this would suggest the observed habitat differences between the northern and southern populations are underscored by maintenance of a specific climatic niche via climatic niche tracking. We expect to find substantial niche overlap between northern and southern populations if the niche is conserved. Alternatively, under a scenario of niche divergence we can infer

that the climatic niche has shifted. The shift may be in one or both populations, and it may be adaptive or plastic, either driven by local adaptation or by the availability of realized niche space. With niche divergence we expect to find little or no evidence of niche overlap.

Through the assessment of niche dynamics and gene flow across this region at the population-level for a single species, we are able to test the mechanism by which the species pump has acted to generate avian species diversity.

Methods

Sampling

We obtained occurrence data for *Cossypha caffra* from throughout their distribution from GBIF and limited our search to vouchered specimens (GBIF.org 2020). We obtained blood or tissue samples for *Cossypha caffra* from our own fieldwork and from museum collections. We included samples from throughout the geographic range of each of the four subspecies; *C. caffra caffra* (Linnaeus, 1771) distributed throughout South Africa, Lesotho, Zimbabwe, Mozambique; *C. c. iolaema* (Reichenow 1900) found in Mozambique, Malawi, Uganda, and Sudan; *C. c. kivuensis* (Schouteden 1937) which is distributed in Uganda, DR Congo, Rwanda, and Tanzania; and *C. c. namaquensis* (Sclater WL 1911) which is found in Namibia and northwestern South Africa.

Molecular methods and data quality

Total genomic DNA was extracted using a Quiagen DnEasy kit according to manufacturer protocols. Building on a previous dataset (Wogan et al. 2020), we genotyped 14 highly polymorphic microsatellite loci (Wogan et al. 2015; Wogan et al. 2020) following the same protocols. We used Microchecker (van Oosterhout et al. 2004) to check for evidence of null alleles, large allele dropout, or genotyping errors due to allelic stutter, and we calculated allelic richness, expected and observed heterozygosity, and theta for each locus using the R package StrataG (Archer et al. 2017).

Population structure and gene flow

Genetic diversity and differentiation

For each subspecies we calculated the number of private alleles, expected and observed heterozygosity, allelic richness, and theta (an F_{ST} estimator), and then evaluated evidence for population differentiation between them. For population differentiation tests, we calculated F_{ST} , Joost's D , X^2 , and G_{ST} measures with 1000 replicates to estimate overall and pairwise differentiation. All of these analyses were carried out in the R package StrataG (Archer et al. 2017).

Population structure

To evaluate if there is evidence of admixture between the northern and southern resident populations, we used an admixture model, testing k values from 2 to 6 with 20 replicates at each k , with a burnin of 10,000 steps and 100,000 steps post burnin in Structure (Pritchard et al. 2000). We used ParallelStructure (Besnier and Glover 2013) to implement the runs on the CIPRES cluster (Miller et al. 2010). To estimate k we employed the deltaK method of Evanno (Evanno et al. 2005), and visualized the results using pophelper (Francis 2017).

Ancestry class assignment

We assessed the ancestry of each individual by statistically assigning them to an ancestry class (parental southern, parental northern, F1, F2+, backcross) to better understand the nature of admixture in this species. We used the Bayesian assignment method implemented in NewHybrids v. 1.1 (Anderson and Thompson 2002; Anderson 2008) and ran three replicates, each with Jeffrey's prior for θ and π , with a post burn-in MCMC chain of 300,000 to 500,000 steps to ensure that it had achieved stationarity, after which we assessed congruence between runs, and then selected one replicate to plot using the scatterpie R package (Yu 2021).

Estimates of gene flow among Southern and Northern populations

To capture estimates of gene flow between the northern and southern populations of *Cossypha caffra*, we used a coalescent approach as implemented in migrate-n (Beerli 2009). We implemented five replicate runs using a Brownian motion msat model, setting θ as a draw from a uniform random, and migration using an F_{ST} based estimate (Beerli and Felsenstein 1999) with the mutation rate estimated from the data. We performed these analyses on the CIPRES cluster (Miller et al. 2010).

Spatial connectivity between Northern and Southern populations

Spatial genetic connectivity

We used graph theory to estimate genetic connectivity among populations. We used the conditional genetic distance statistic (cGD) (Dyer and Nason 2004), and then visualized it as a population graph using the R packages gstudio and popgraph (Dyer 2009). The nodes in the graph represent sampled populations, and the edges represent genetic connection (Dyer and Nason 2004; Miles et al. 2018). We used 100 replicate bootstrapping to gauge

the stability and statistical support for each edge in the graph (Kutnjak et al. 2014).

Spatial genetic connectivity through time

We generated environmental niche models (ENMs) for *Cossypha caffra*. We projected ENMs onto paleoclimate reconstructions to assess the suitability of climate for the two delineated genetic clusters corresponding to north and south in a spatially explicit framework. We generated ENMs for the present using MaxEnt v. 3.4.1 (Phillips et al. 2004; Phillips and Dudik 2008), and hindcast the model on to paleoclimatic reconstructions. We used a downscaled HADCM3 global circulation model at a resolution of c. 4 km grid cells (0.0466667) from which we generated 62 time slices dating from 120 ka to the present for eight bioclimatic variables: annual mean temperature; temperature seasonality; mean temperature of the warmest quarter; mean temperature of the coldest quarter; annual precipitation; precipitation seasonality; precipitation of the wettest quarter; and precipitation of the driest quarter. We generated time slices in 4 ka increments from 120 ka to 88 ka, 2 ka increments from 88–22 ka, and 1 ka increments from 22 ka to present (Fuchs et al. 2013; Voelker et al. 2021). We combined our sampling geocoordinates with the GBIF occurrence data. We removed duplicate points from the same grid cell and then built a contemporary MaxEnt model with the regularization set to 0.001, and with 25% of the samples set aside for testing, and we then used jack-knifing to evaluate the contribution of each bioclimatic variable to the model. We projected this model onto our paleoclimatic layers. Using all 62 layers, we calculated static areas of stability, i.e. stacked areas where suitability is consistently predicted to be high through time (Hugall et al. 2002; Carnaval et al. 2009) as well as dynamic species refugia, in which areas of stability can shift across the landscape between adjacent time periods (Graham et al. 2010). In dynamic refugia, connectivity is assessed by classifying grid cells as stable if the environmental suitability allows persistence in the cell or dispersal to the cell from other cells (Graham et al. 2010; Rosauer et al. 2015). The probability of dispersal is estimated as a linear function of the distance between two grid cells (Graham et al. 2010). We tested a several range-shift/dispersal rates (10–1000 m per year). *C. caffra* adults are territorial and pair for life, and defend small territories of 0.05 to 0.75 ha year round (Keith et al. 1992; Bonnevie et al. 2003; Hockey et al. 2005; Clement and Rose 2015), and given that these estimates are delimiting movement per year rather than per generation, rates on the low-end are expected to better capture these spatial dynamics (Fuchs et al. 2013; Potter et al. 2018).

To assess movement through time, we used an explicit dispersal model to generate maps of accessibility given a northern versus a southern origin of Cape Robin using the KISSmig R package (Nobis and Normand 2014). For these analyses we built a dynamic environment using the 62

suitability maps, and then ran simulations with 200–500 iterations per timeslice with the first occurrence (FOC) or number of occurrences (NOC) options allowing for stochasticity among iterations, and set northern or southern origins, and then calculated accessibility in order to evaluate dispersal movement through time.

Niche divergence or conservatism

Niche overlap and equivalency

Using the GBIF data in combination with records from our work, we assessed niche breadth using two measures, B1 and B2 (Levins 1968; Warren et al. 2019), and niche overlap between northern and southern populations of *Cossypha caffra*. We calculated niche overlap using Schoener's D (Schoener 1968) and a modified Hellinger's I statistics (Warren et al. 2008), and then performed tests of niche equivalency and niche similarity (Warren et al. 2008). Niche equivalency tests if niches are drawn from the same distribution by measuring the constancy of overlap between niches when occurrence data are pooled and split randomly. Niche similarity tests if the occupied niche in each range more similar to the occupied range in the other than expected by chance and assesses niche overlap while taking into account the background environment (Warren et al. 2008; Broennimann et al. 2012). To ensure that our inference of niche overlap is not solely driven by geographic background we also assessed overlap using Schoener's D and Hellinger's I in n-dimensional environmental space (Broennimann et al. 2012). To assess if the range disjunction is driven by significant ecological barriers such as steep environmental gradients or unsuitable intervening habitats, we used the linear range break test (Glor and Warren 2010). The linear range break test gauges if a geographic break between ranges is due to the presence of a steep environmental gradient. It does this by making the prediction that ENMs on either side of the putative barrier will be more divergent than ENMs generated from a random geographic subdivisions of pooled samples. For tests of identity and similarity and the range break test, we ran 100 replicates using maxent models (if the test required them), and performed all of the niche analyses using the ENMtools R package (Warren et al. 2010).

Results

Our sampling consisted of 335 individuals including representatives of all currently recognized *Cossypha caffra* subspecies: *C. caffra caffra*, *C. c. iolaema*, *C. c. kivuensis*, and *C. c. namaquensis* (Fig. 1). This sampling includes genotyping for an additional 74 individuals for the same 14 microsatellite loci as in Wogan et al. (2020), to include expanded sampling in southern Africa from Namibia and South Africa, and focused sampling from populations in northern Mozambique, Malawi, Tanzania, and the Demo-

cratic Republic of Congo. We did not recover evidence of null alleles, large allele dropout, or genotyping errors due to allelic stutter in the msat loci with our expanded sampling.

Population structure and gene flow

Estimates of genetic diversity and differentiation

The number of alleles for each locus ranged from 10 to 35, and allelic richness ranged from 0.03 to 0.14 (Suppl. material 1: table S1). We found that most of the loci had an observed heterozygosity approaching expected heterozygosity (Suppl. material 1: table S1). Two loci (78, c233) had increased missing data for the northern populations, and including and excluding these loci did not affect the results, and therefore our results are based on the full dataset.

Using the defined subspecies as our pre-defined populations, we found that permutation tests provided evidence for population differentiation among the subspecies using Joost's D (0.2056, p-value: 0.0009) and ChiSq (3118.6682, p-value: 0.0009) metrics. Pairwise comparisons supported this finding for all subspecies (Suppl. material 1: table S2). The low samples size of *Cossypha caffra kivuensis* precluded pairwise F_{ST} -based comparisons for that taxon, but F_{ST} and G_{ST} -based metrics support population differentiation among *C. caffra caffra*, *C. caffra iolaema*, and *C. caffra namaquensis* (Suppl. material 1: table S2).

Population analyses

The population analyses identified a best-fit of three clusters within the dataset (Fig. 2, Suppl. material 1: fig. S1). Among the northern populations, all samples form a single cluster, and therefore are not concordant with the subspecific taxonomy recognizing *C. caffra iolaema* and *C. caffra kivuensis* (Fig. 2). Two population clusters were identified within Southern Africa. The genetic clusters and subspecies boundaries in southern Africa are not concordant, and the two differentiated genetic clusters each include individuals of both subspecies; *Cossypha caffra caffra*, and *Cossypha caffra namaquensis*. Based on the initial clustering under $k = 2$, the most substantial genetic divide in the data is between northern and southern populations, and these two major clusters are identified consistently across the six potential values of k evaluated.

Admixture and ancestry

We recovered a signal suggesting that there is admixture between the northern and southern regions, with ancestry proportions for two individuals representing both southern clusters amidst the northern populations, and

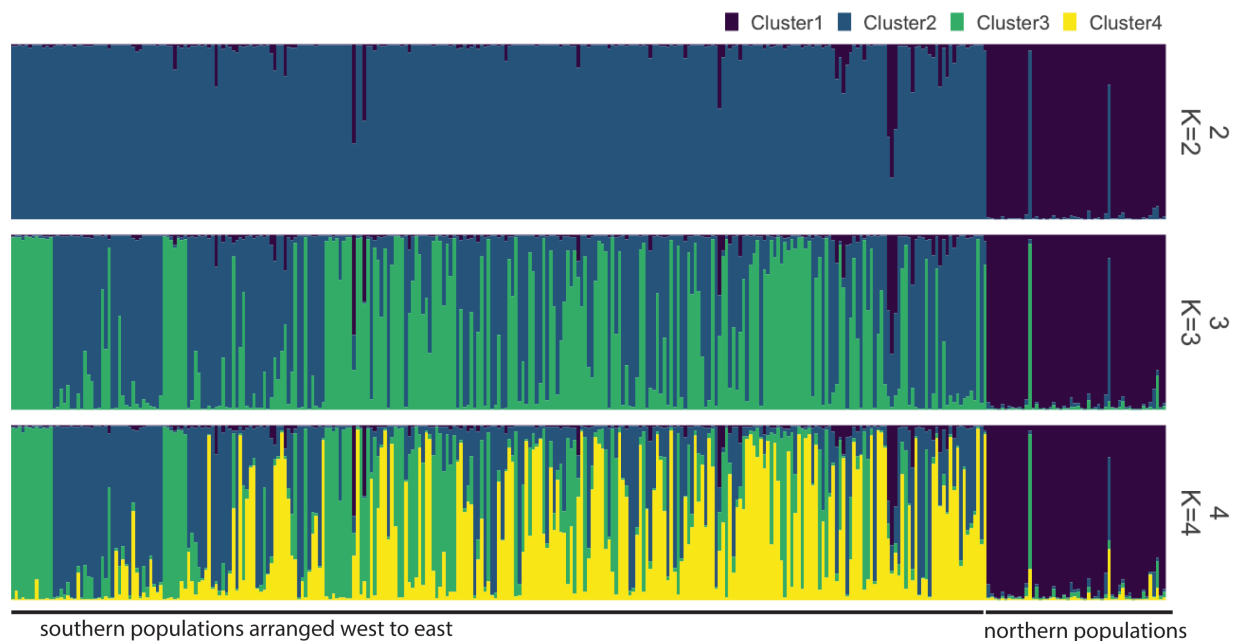


Figure 2. Results from population structure analyses for *Cossypha caffra* depicting the clustering recovered for k -values of 2 to 4. The analyses recovered a best fit of three clusters in the data. These correspond with two clusters in southern Africa (South Africa, Namibia, Mozambique) and one encompassing all of the northern populations (Malawi, Tanzania, Democratic Republic of Congo).

northern ancestry identified among the southern African populations (Fig. 2). The northern ancestry in the south is most pronounced in populations in the east (Fig. 2).

Most individuals were assigned to an ancestry category with high certainty ($> .80$). The results assigned 247 samples as southern parentals, 27 samples assigned as northern parentals, and 15 samples were assigned as F2s. No individuals were assessed to be F1s or back-crosses. *C. caffra caffra* and *C. caffra namaquensis* individuals were assigned as southern parentals or F2s. *C. caffra iolaema* samples were assigned as northern parentals or F2s, and of the three *C. caffra kivuensis* samples, one was assigned with certainty as an F2, while the others were assigned with ambiguity as either a northern parental or an F2. When probabilities for each of the ancestry categories are plotted with respect to geography, the assignments suggest that there is a distinctive divide between northern and southern assignment near the Mozambique – Tanzania border (Fig. 3A). While no individuals were identified as F1 hybrids, F2s are distributed in both northern and southern populations. Although no individuals were assigned as backcrosses, in a few populations (all northern) the probability for the backcrossed category is notable, suggesting that within those populations there is statistical probability supporting backcrossing (Fig. 3A). This may reflect the reduced resolution that arises when distinguishing among classifications of F2s, first generation backcrosses, and older backcrosses (Pereira and Wake 2009). Hence, our identified F2s may indeed belong to older backcross categories reflecting a longer period of isolation between northern and southern populations. We also recovered a few northern parental individuals within the southern populations.

Estimates of gene flow

The estimates of gene flow between the northern and southern populations of *C. caffra* suggest highly asymmetric patterns of gene flow between the northern and southern populations, with northern gene flow into southern populations at ten-fold greater levels than vice-versa (N to S 0.199, S to N 0.013) (Fig. 3A).

Spatial genetic connectivity

We recovered 13 stable edges (Suppl. material 1: table S3). The popgraph analysis recovered evidence of north-south genetic connectivity between the population in the Democratic Republic of Congo (*C. caffra kivuensis*) and both the South African grasslands populations of *C. c. caffra*, (Fig. 3B), and *C. caffra namaquensis* from Namibia. There is also north-south genetic connectivity between Malawi populations of *C. caffra iolaema* and South African grasslands populations of *C. c. caffra*. The populations in western South Africa (i.e. to the west of the Nama Karoo) do not directly exchange genes with the northern populations, instead gene exchange is mediated through the grasslands populations of *C. c. caffra* or the Namibian populations of *C. caffra namaquensis*. Genetic connectivity is indicated among all sampled northern populations (DRC and Malawi; Fig. 3B).

Spatial genetic connectivity through time

We combined occurrence points from our sampling with vouchered occurrence points from GBIF for a total of 794 occurrences. These points are distributed throughout the

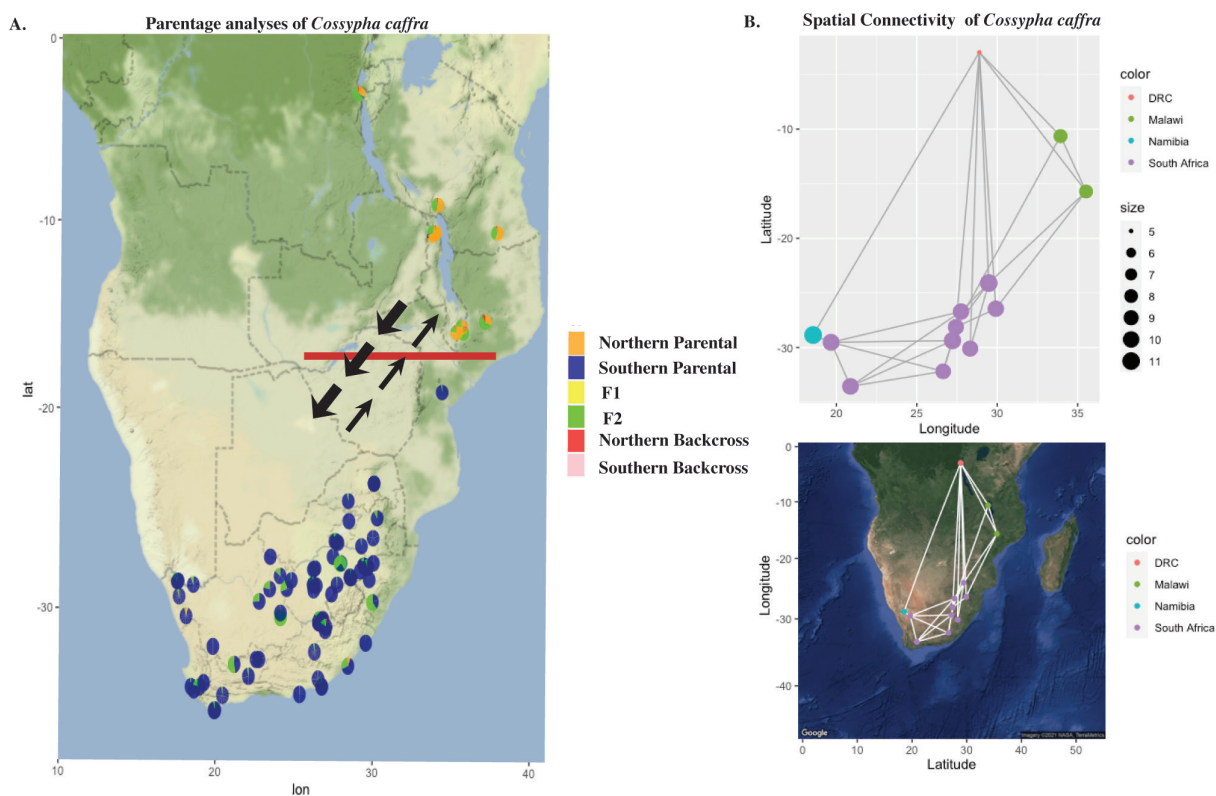


Figure 3. Spatial Genetic Connectivity of *Cossypha caffra* populations. Panel A ScatterPie charts depicting the geographic distribution of ancestry categories. The red bar at the Mozambique-Tanzania border depicts the divide between the northern and southern lineages. Black arrows depict the intensity of gene flow between northern and southern lineages. Panel B (top) depicts a population graph in which nodes are sampling localities and edges represent gene flow, the nodes are scaled by sample size. Panel B (bottom) shows the network within geographical context.

range of *Cossypha caffra* (Fig. 1) and as such should encompass the range of environmental conditions experienced by the species. The contemporary ENM had high predictive capacity with an AUC score of 0.958. Jackknife analyses revealed that annual mean temperature (bioclim 1) and precipitation of the driest quarter (bioclim 17) are highly relevant contributors to the distribution occupied by *C. caffra*. ENMs built by hindcasting the ENM to our 62 downscaled paleoclimate snapshots revealed highly dynamic suitability, characterized by dramatic contractions and expansions in both the northern and southern portions of the *Cossypha caffra* range (Suppl. material 2) and intermittent suitability and connectivity between the Northern and Southern populations (Suppl. material 2). Static refugia are predicted to have existed in South Africa, and across the Zimbabwe-Mozambique, the Tanzania-Malawi, and the Democratic Republic of Congo-Tanzania borders, and in Kenya (Fig. 4A). Notable is the lack of stable areas predicted between the northern regions and southern regions (Fig. 4A). Dynamic refugia models at lower dispersal/ range-shift rates (<50 m per year) are similar to the stable refugia, but indicate more substantial stable areas predicted in between the northern and southern regions (Fig. 4B, Suppl. material 1: fig. S2). At higher range-shift values the estimated refugia expand to encompass most of sub Saharan Africa (Suppl. material 1: fig. S2). Both static and shifting regions of stability are also predicted in

Ethiopia and Madagascar, although *Cossypha caffra* is not distributed in either region.

The dispersal models, which are integrated across the past 120 thousand years were similar for both the Northern and the Southern Origin hypotheses, revealing that there are two connected areas, one consisting of South Africa, southern Namibia, Zimbabwe and Mozambique and another comprising a northern connected region encompassing the Democratic Republic of Congo, Malawi, Kenya, and Tanzania (Fig. 5A). There is a disjunction at the Mozambique-Tanzania border separating the northern and southern areas of connectivity (Fig. 5). The maps of accessibility suggest that dispersal is feasible between these populations, and the realized distribution of *C. caffra* is recapitulated in the approximated dispersal-based distribution (Suppl. material 1: fig. S3). Colonization of the Savanna biome was rare, and no colonization is predicted in potentially suitable habitat that exists outside of the species realized range, suggesting that dispersal lag and barriers exist to shape the realized range.

Niche overlap and equivalency

ENMs generated for the northern and southern populations independently revealed that for the northern populations, there is a corridor of environmental suitability between eastern Africa and southern Africa leading to the southern

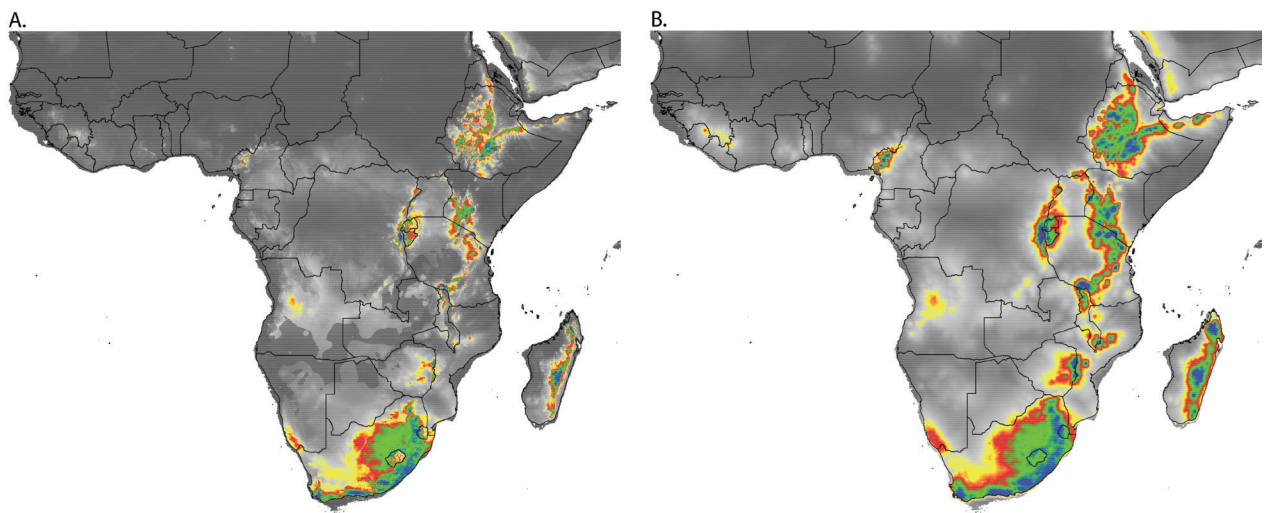


Figure 4. Estimates of species refugia for *Cossypha caffra*. Panel A depicts the stable species refugia. Panel B depicts shifting species refugia estimated at a shift rate of 10 m per year. Both are estimates based on 62 hindcast projections over the past 120 thousand years.

Integrated dispersal models for *Cossypha caffra*

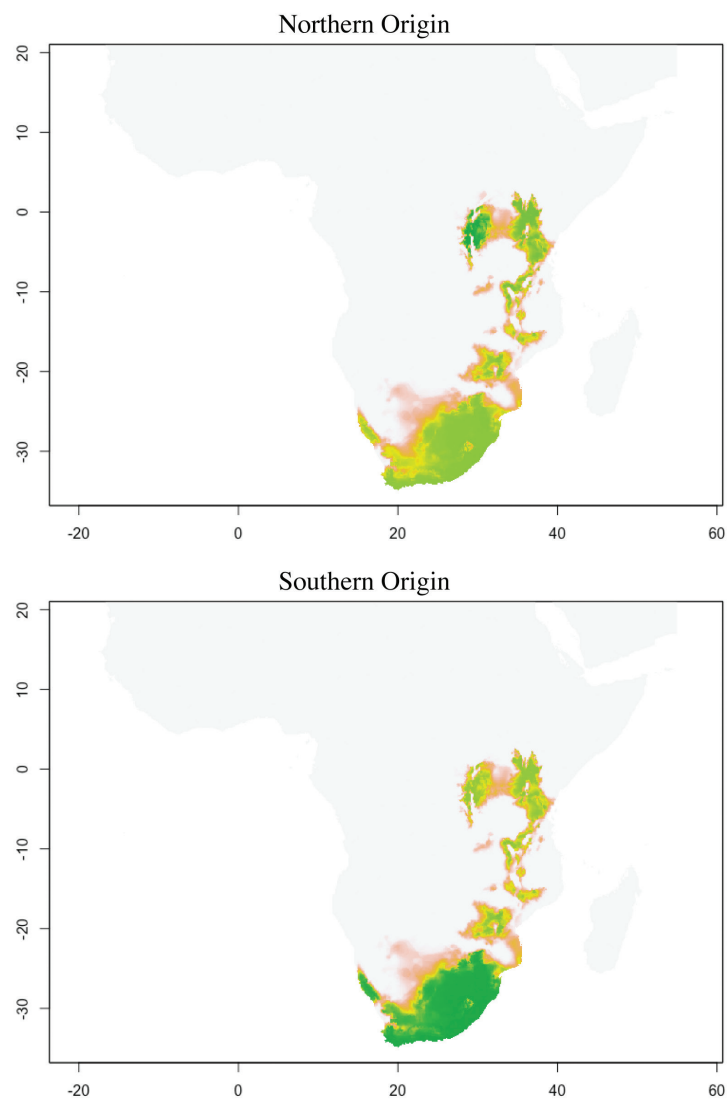


Figure 5. Integrated estimates of dispersal between disjunct populations of *Cossypha caffra*. These are migration surfaces integrated over the past 120 thousand years with either a northern (top) or southern (bottom) origin. The colors reflect the proportion of iterations in which there is an occurrence dark green (highest proportion of occurrence across iterations) to pink (rare occurrence) to white (no occurrence).

populations (Fig. 6), while for the southern populations, that corridor is considerably more fragmented north of the Mozambique-Tanzania border (Fig. 6A). The model for the southern populations also reveals climatic suitability in the highly arid regions of North Africa (Fig. 6). The results from the ENM-based and direct environment-based identity test were statistically significant (p-value of 0.01 for all measures) (Fig. 6B). In all instances, the observed measure, indicated by the dashed line, falls well outside of the simulated distributions (Fig. 7A). Furthermore, the model-based niche breadth for both populations is estimated to be high (northern: 0.906, southern: 0.942), while environmental space niche breadth is considerably lower (northern: 0.175, southern: 0.384), indicating that populations in both parts of the range have narrow fundamental niches that encompass a common realized set of environmental spaces (Fig. 7B). Estimates of niche overlap based on ENMs ($D = 0.191$, $I = 0.426$, Spearman's Rank Correlation = -0.215) and estimates based directly in environmental space ($D = 0.245$, $I = 0.411$, Spearman's Rank Correlation = -0.228) suggest little overlap in niche space between the northern and southern populations.

The symmetric background tests, both those based on ENMs and those based on environmental space, are also statistically significant for measures of Schoener's D and Hellinger's I (p-value of 0.01). The Spearman rank correlation has conflicting support, with the ENM-based measure not statistically significant (0.069), and the direct environment-based measure statistically significant (p-value of 0.01) (Suppl. material 1: fig. S4). When corrected for the available environmental space, the results of the identity test for both D and I were statistically significant ($D = 0.155$ p-value 0.02; $I = 0.3$ p-value 0.01) (Suppl. material 1: fig. S4) supporting niche divergence between the northern and southern populations. Conversely, the background similarity test revealed that the background environment was not significantly different in environmental space ($D = 0.155$ p-value 0.08; $I = 0.3$ p-value 0.08) (Suppl. material 1: fig. S4). Furthermore,

the linear range break test was not statistically significant, which means that there is no support for a steep environmental gradient within the range. In combination, this indicates that the northern and southern geographic environments are not more different than expected by chance, supporting background environmental similarity (Suppl. material 1: fig. S5).

Discussion

The disjunct resident populations of *Cossypha caffra* are distributed across a large latitudinal and elevational gradient. Within *C. caffra*, genetic diversity is structured with distinct northern and southern populations, and with the primary genetic break delineating populations located in eastern Africa near the Mozambique – Tanzania border. The rates of gene flow are highly asymmetric, with a ten-fold higher difference in north to south versus south to north estimates of gene flow. Genetic connectivity indicates that most of the north-south gene flow occurs from northern populations into the southern populations distributed across central and eastern South Africa, those inhabiting grassland and savanna habitats.

Other species have similar genetic breaks in eastern Africa (Fuchs et al. 2011; Lorenzen et al. 2012; Bertola et al. 2016; Bryja et al. 2017; Barratt et al. 2018), and among birds this has previously been documented in arid adapted Fiscal Shrikes (Fuchs et al. 2011). The *Cossypha caffra* genetic break is broadly consistent with the East African suture zone identified for mammals (Lorenzen et al. 2012). The genetic break also roughly corresponds with the division between two traditionally recognized montane regions for bird endemism: the Eastern Arc mountains, and the Tanganyika Rift/southern Africa region (Moreau 1966; Fjelds  and Bowie 2008). This suggests that, similar to the Olive Sunbird, *Nectarinia olivacea* (Bowie et al. 2004), the Eastern Arc mountains have served as a source for the southern African *C. caffra* populations.

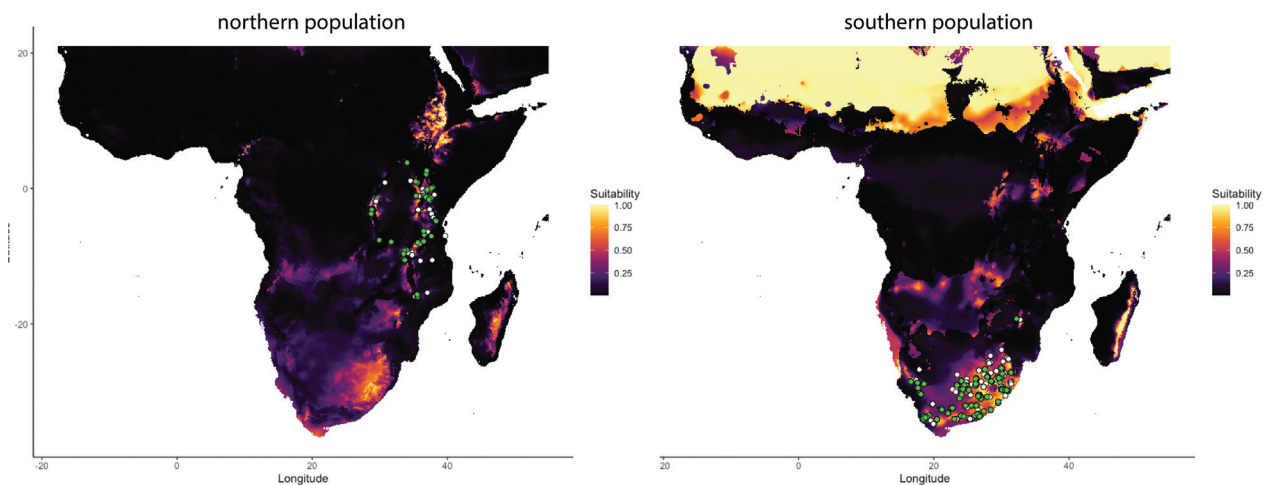
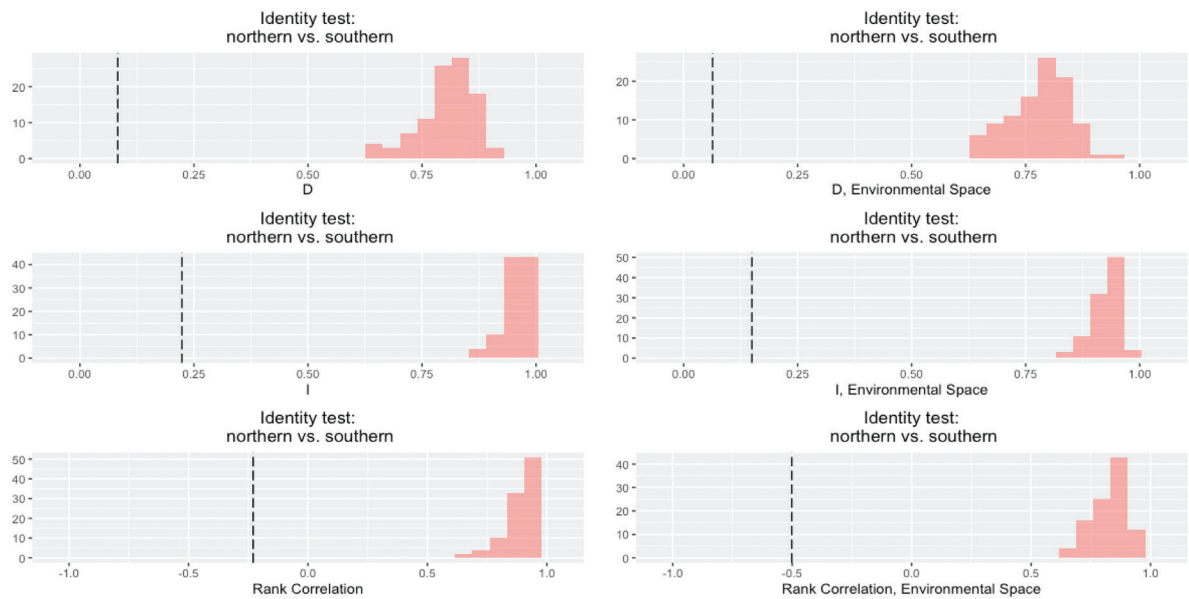


Figure 6. Maps depicting the climatic suitability of the northern and southern populations of *Cossypha caffra*. Colors scale from light yellow (highly suitable) to black (not suitable). The points are the training (green) and testing (white) sampling points used for estimating environmental suitability.

A.



B.

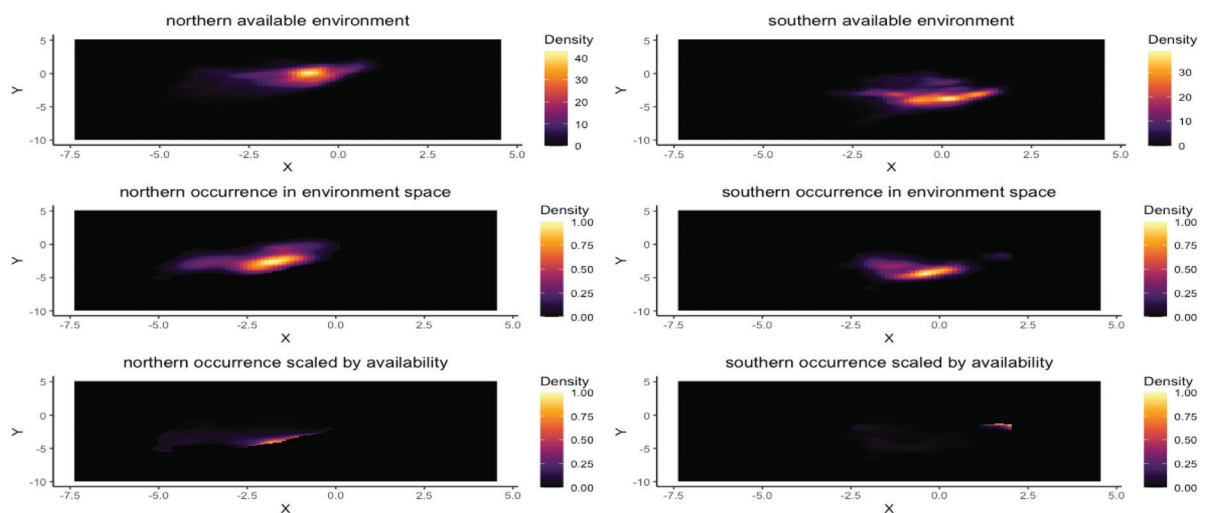


Figure 7. Niche divergence. Panel A. The result of tests of Identity for Schoener's D and modified Hellinger's I statistics. The left three plots are generated from ENMs, while the right three plots are in environmental space. The dashed lines represent the observed value compared against a histogram that is the distribution generated through a resampling scheme. Panel B. Quantification of niche identity and background tests in environmental space, where the axes (x,y) represent the first two Principal Components of environmental space.

Recent work has demonstrated that highly dynamic paleoclimatic perturbations arising from complex El Niño Southern Ocean oscillation (ENSO) have been linked to mammalian dispersal routes and corridors throughout Sub-Saharan Africa (Kaboth-Bahr et al. 2021), and we expect that the ENSO would similarly affect many species of birds. The dispersal modelled for *C. caffra* over the past 120 ka suggests a corridor between the northern and southern populations where climatic conditions have been largely suitable throughout relatively recent climatic oscillations. However, the modeled geographic break in habitat suitability and the observed genetic break are concordant for *C. caffra*, suggesting that a distinct discontinuity due to poor environmental suitability near the Mozambique-Tanzania border has driven genetic differentiation between the northern and southern resident populations. Indeed,

individual niche models for the northern populations indicate a corridor of suitable environmental conditions connecting the northern populations to the southern populations, however, that same corridor does not exist for the southern populations. Instead, the southern populations lack a suitable environmental space that would allow them to easily move north. Thus for *C. caffra*, we can infer that the habitat barrier near the Mozambique-Tanzania border may act as a strong environmental filter that acts to limit northward dispersal by individuals from southern aridland adapted populations.

These findings are congruent with the hypothesized species pump paradigm as a species-generating force contributing to the high levels of avian species diversity in southern Africa, although under a modified scenario. Under this paradigm, the "species pump" for *C. caffra*

involved the dispersal of the northern population individuals along the north-south corridor, resulting in the establishment of the southern populations. Given the lack of northward dispersal we would, under our modified species pump hypothesis, suggest that the southern populations have over time diverged and experienced niche evolution, giving rise to the locally adapted aridland populations that characterize the southern African populations of *C. caffra*.

All of our niche-based analyses support a scenario by which the northern and southern populations of *C. caffra* have divergent climatic niches, despite the overall similarity of the background environments between the northern and southern regions. This suggests that these populations either occupy different parts of their fundamental niches, or they have become locally adapted. To more fully explore the idea that these species are locally adapted, physiological assays and assessments of phenotypic differentiation would be required. Additionally, the use of genomic data to discern whether there are loci that exhibit differential associations with environmental gradient elements would potentially provide powerful insights into the eco-evolutionary dynamics at play in *C. caffra* diversification.

If the species pump paradigm has been acting as we hypothesize, then we would expect that multiple species of birds with similar geographically broad and environmentally diverse ranges will share the pattern recovered for *C. caffra*. Based on very limited evidence that southern to northern colonizations have occurred in African bird lineages (Voelker et al. 2014, 2016), we expect that northern to southern colonizations will predominate. As there are many bird species with ranges that span the Mozambique-Tanzania border, additional studies will help determine if this region is an avian “species generating” region *sensu* Hall and Moreau (1970). We should note that our modified version of the species pump hypothesis is specifically centered around aridland taxa, with forest expansion acting as an isolating barrier among northern and southern aridland lineages (Voelker et al. 2010).

In addition to the ecological divergence recovered for *C. caffra* in this study, others have suggested that shifts in habitat preference may be driven by biotic interaction with congeners, specifically *C. heuglini* (Hall and Moreau 1970). It has been noted that where the two species co-occur (i.e. northern populations), *C. caffra* is restricted to montane habitat (Hall and Moreau 1970). Testing these types of biotic interactions may yield additional insights into the proximate causes of ecological divergence.

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Author Contributions

Designed the study: GOUW, RCKB, GV, Collected samples: RCKB, GV, PK, Generated Data: GOUW, Analyzed Data: GOUW, TJ, Wrote the manuscript: GOUW, RCKB, GV, Edited and approved the manuscript: GOUW, TJ, PK, RCKB, GV Obtained Funding to support the research: RCKB, GV.

Data Accessibility

Data in this paper are available in the Suppl. material 1.

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Supplementary materials

Supplementary material 1

Supplementary tables (tables S1–S3) and figures (figs S1–S3) (.pdf)

Link: <https://doi.org/10.21425/fob.17.132679.suppl1>

Supplementary material 2

Animated GIF image (.gif)

Link: <https://doi.org/10.21425/fob.17.132679.suppl2>