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RESEARCH ARTICLE

Southern Africa's Great Escarpment as an amphitheater of climate-driven diversification and a buffer against future climate change in bats

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Abstract

Hosting 1460 plant and 126 vertebrate endemic species, the Great Escarpment (hereafter, Escarpment) forms a semi-circular "amphitheater" of mountains girdling southern Africa from arid west to temperate east. Since arid and temperate biota are usually studied separately, earlier studies overlooked the biogeographical importance of the Escarpment as a whole. Bats disperse more widely than other mammalian taxa, with related species and intraspecific lineages occupying both arid and temperate highlands of the Escarpment, providing an excellent model to address this knowledge gap. We investigated patterns of speciation and micro-endemism from modeled past, present, and future distributions in six clades of southern African bats from three families (Rhinolophidae, Cistugidae, and Vespertilionidae) having different crown ages (Pleistocene to Miocene) and biome affiliations (temperate to arid). We estimated mtDNA relaxed clock dates of key divergence events across the six clades in relation both to biogeographical features and patterns of phenotypic variation in crania, bacula and echolocation calls. In horseshoe bats (Rhinolophidae), both the western and eastern "arms" of the Escarpment have facilitated dispersals from the Afrotropics into southern Africa. Pleistocene and pre-Pleistocene "species

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pumps" and temperate refugia explained observed patterns of speciation, intraspecific divergence and, in two cases, mtDNA introgression. The Maloti-Drakensberg is a center of micro-endemism for bats, housing three newly described or undescribed species. Vicariance across biogeographic barriers gave rise to 29 micro-endemic species and intraspecific lineages whose distributions were congruent with those identified in other phytogeographic and zoogeographic studies. Although Köppen–Geiger climate models predict a widespread replacement of current temperate ecosystems in southern Africa by tropical or arid ecosystems by 2070–2100, future climate Maxent models for 13 bat species (all but one of those analyzed above) showed minimal range changes in temperate species from the eastern Escarpment by 2070, possibly due to the buffering effect of mountains to climate change.

KEYWORDS
Afromontane, baculum, biodiversity evolution, Chiroptera, craniometric, cytochrome-b, echolocation frequency, geographical range, phenotype

1 | INTRODUCTION

The uplift and easterly tilting of the southern African Escarpment ca. 23 million years ago (Ma), and the formation of the Benguela Current ca. 11 Ma, resulted in strong aridity and elevation gradients, with arid and semi-arid (hereafter, "arid") highlands in the west and temperate high mountains in the east, rising to 3482 m in the Maloti Drakensberg (Couvreur et al., 2021; Partridge & Maud, 1987). Including the Cape Fold Belt (CFB) on its southern edge, the 5000 km long Escarpment hosts over 8500 plant species, including 1460 endemic plants, and at least 126 endemic vertebrate species (Clark, Barker, & Mucina, 2011a; Huntley, 2023; Mendelsohn et al., 2023).

Both ecological and evolutionary "actors" explain the exceptionally high diversity and endemism of this semi-circular, subcontinental "amphitheater" of highlands. Ecologically distinct sections ("tiers") of the Escarpment correspond with recognized biomes and ecoregions (Dinerstein et al., 2017; Table S1; Figure 1a). Spanning temperate (northern) to arid (southern) biomes, the Highlands and Escarpments of Angola and Namibia (HEAN; Mendelsohn et al., 2023) form the western rim. The southern Escarpment is formed by the Richtersveld, Hantam–Roggeveld and Nuweveldberge highlands in the Nama Karoo and Succulent Karoo biomes of South Africa (Mucina & Rutherford, 2006). South of the southern Escarpment, separated by the Little Karoo semi-desert, lie the geologically distinct CFB mountains covering the Core of the Greater Cape Floristic Region (CFR) and Fynbos Biome (Mucina & Rutherford, 2006). The eastern rim of the Escarpment coincides with the Sneeuberg and Maloti Drakensberg (= Drakensberg Centre for Plant Endemism; Carbutt, 2019) mountains which continue northwards as the Greater Midlands (Carbutt, 2023), Limpopo–Mpumalanga–Eswatini Escarpment (LMEE; Clark et al., 2022) and Soutpansberg (Hahn, 2017; Van Wyk & Smith, 2001). The Manica Highlands of Zimbabwe and Mozambique (Chimanimani-Nyanga centers of plant endemism (CPE); Clark et al., 2017; Van Wyk & Smith, 2001) can be regarded as an extension of the Escarpment (Clark, Barker, & Mucina, 2011a), and also provide a bridge with the Eastern Afromontane Biodiversity Hotspot (Mittermeier et al., 2011), which extends north to Ethiopia and Arabia, encompassing the South-East African Montane Archipelago ecoregion (SEAMA; Bayliss et al., 2024), Eastern Arc Mountains (EAM) and the East African Rift System (EARS; Figure 1a).

Tectonics, topography, and past climate change have shaped evolutionary processes like dispersal, vicariance, extinction, adaptation, and speciation (Couvreur et al., 2021; Rangel et al., 2018; Voelker, 1999). Tectonic processes explain the evolution of the Maloti Drakensberg flora from the Cape flora, and subsequent dispersal and radiation into newly formed tropical African mountains over the past 17 Ma (Galley et al., 2007). The formation and extension of the East African Rift from the Miocene (23–5.3 Ma) to the Pleistocene (2.6–0.012 Ma) led to forest fragmentation and the vicariance of highland from ancestral lowland taxa, for example, in wood mice, *Hylomyscus* (Nicolas et al., 2020). The early Pleistocene (ca. 2.5 Ma) formation of the Ethiopian Rift Valley explained vicariance between ancestral western and eastern species in the Ethiopian-endemic rodent genus *Stenocephalemys* (Bryja et al., 2018).

Past climate and vegetation change were critical drivers of Afromontane diversity, particularly during the Pleistocene (2.6 Ma–18 Ka) and Pliocene (5.3–2.6 Ma) periods. Pliocene forest contraction explains biogeographical patterns in Afromontane birds (Voelker et al., 2010; Outlaw et al., 2007) and chameleons (Tolley et al., 2011). Analyses of Antarctic marine sediments from dust particles from southern African deserts indicated a 5°C decline in global temperature in the early Pleistocene, and the pronounced ca. 100,000-year (100 Ka) periodicity of cold and warm cycles (Milankovitch cycles) after the mid-Pleistocene transition event (ca. 900 Ka), leading up to the last glacial maximum (LGM) at about 18 Ka (Couvreur et al., 2021; DeMenocal, 1995, 2004; Schefuss et al., 2003). Geomorphological and archeological evidence confirms the existence of cold cycles (5–10°C lower than

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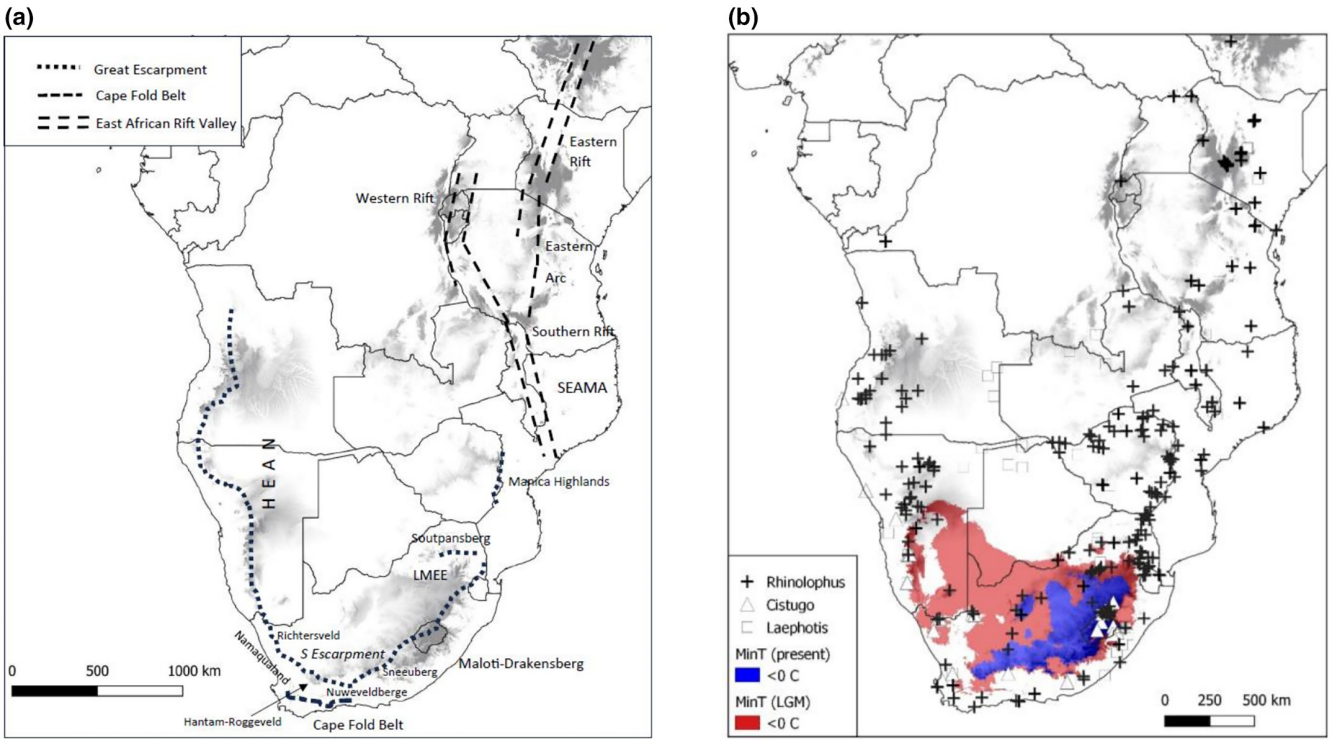


FIGURE 1 Maps of southern, central, and eastern Africa showing (a) topographical features referred to in this study (see text for details), and (b) the extent of minimum monthly temperatures (bioclim6) <0°C from present and past (last glacial maximum [LGM]) models (from Worldclim; https://www.worldclim.com/; see Methods for more details). Gray or darker shading in both maps indicates mountains >1200 m in elevation. In (a), the acronym HEAN stands for the Highlands and Escarpments of Angola and Namibia (Mendelsohn et al., 2023); SEAMA stands for the South-East African Montane Archipelago (Bayliss et al., 2024); LMEE stands for the Limpopo–Mpumalanga–Eswatini Escarpment (Clark et al., 2022). The map in (b) shows distribution points of horseshoe bats, *Rhinolophus* (crosses), wing-gland bats, *Cistugo* (open triangles) and long-eared bats, *Laephotis* (open squares) based on morphological and molecular results from this study and from published a GenBank cyt-b sequences. In (b), minimum monthly temperatures <0°C indicated for the present (blue) and LGM (red), approximating the extent of frost (and hence temperate grasslands) currently and during the LGM (idea from Brain, 1985). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

present) and small "niche glaciers" in the Drakensberg of South Africa and Lesotho during the late Pleistocene including the LGM (Fitchett et al., 2016; Grab, 1996; Harper, 1969). Pleistocene climatic fluctuations drove repeated expansion and contraction of Afromontane habitats on adjacent mountains, resulting in allopatric or peripatric vicariance and speciation during periods of isolation (montane refugia mechanism: Bryja et al., 2014; Couvreur et al., 2021; Taylor et al., 2014). During Holocene (0–18 Ka) and Pleistocene hypothermal periods, frost-dependent grasslands extended more widely across southern Africa, possibly connecting species currently restricted either to the western, southern, or eastern Escarpment (Brain, 1985; Figure 1b).

Many studies show the biogeographical connectivity of the southern and eastern sections of the Afromontane Archipelago ("Cape to Cairo Floristic Highway"; Clark, Barker, & Mucina, 2011a) and their importance as either dispersal corridors, "cradles" (high speciation rate) or "museums" (high species persistence) of montane plants and animals (e.g., Clark, Barker, & Mucina, 2011b; Couvreur et al., 2021; Dianat et al., 2024; Fjeldså & Lovett, 1997; Fjeldså et al., 2012; Galley et al., 2007; Lawson et al., 2015; Nicolas et al., 2020; Onditi et al., 2021; Tolley et al., 2011; Taylor et al., 2012, 2014; Voelker et al., 2010, 2021). Fewer studies demonstrate the role of the western Escarpment (HEAN and Richtersveld Mountains of South Africa) in the speciation of arid species (Huntley, 2023; Huntley et al., 2019; Linder et al., 2012; Matthee & Flemming, 2002; Matthee & Robinson, 1996; Mendelsohn et al., 2023; Mills et al., 2011). Biogeographical connections are known to link the Angolan (HEAN) and East African highlands, for example, in rodents (Krásová et al., 2021) and birds (Mills et al., 2011; Vaz da Silva, 2015). However, the evolutionary and biogeographical importance of the entire Escarpment has not been fully investigated previously. Because of their greater dispersal capacity compared with more sedentary taxa, bats are widely distributed across both arid (western) and temperate (southern and eastern) mountains of the Escarpment and therefore provide an excellent model to address this gap.

Because they depend on rocky crevices and caves for roosting, the distribution ranges of several bat species correspond with mountainous areas of the CFB, the Escarpment, and the broader Afromontane Archipelago (Table S2; Figure 1a,b; Monadjem et al., 2020; Schoeman et al., 2013). We define southern Africa to extend from the DRC south of 4°S to South Africa (Monadjem et al., 2020). We use the term "paramontane" to describe bats

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whose distributions encompass either lower and/or higher mountain slopes and plateaux (Fahr & Ebigbo, 2003; Koopman, 1983). We selected six paramontane species groups or genera of bats comprising 14 species from three families of both recognized sub-orders (Pteropodiformes: Rhinolophidae; Vespertilioniformes: Cistugidae, and Vespertilionidae; Table S2). Their combined distribution ranges coincide with high (>1200 m) elevation and major topographic features (Figure 1a,b), and climate zones based on the Köppen–Geiger system (Table S1; Figure S1; Beck et al., 2018). Based on future climate models, temperate conditions (green colors) are expected to contract by 2070–2100 at the expense of more tropical (blue) or arid (red) zones in southern Africa, raising a possible red flag for the conservation impacts of climate change on temperate-adapted fauna and flora in general (Figure S1). For species having an adequate number of occurrence records, we here test this general hypothesis by using Maxent niche models to predict future climate change projected ranges of 13 of the 14 paramontane bat species for 2070 (from IPCC6 models).

Horseshoe bats (*Rhinolophus*) are a diverse group of >100 species, including a growing number of newly discovered cryptic species (Benda & Vallo, 2012; Benda et al., 2024; Curran et al., 2022; Dool et al., 2016, Demos et al., 2019; Monadjem et al., 2020; Taylor et al., 2012, 2018; Uvizl et al., 2024). Six Afrotropical groups are recognized, *capensis*, *darlingi*, *ferrumequinum*, *fumigatus*, *landeri*, and *maclaudi*, of which all but *maclaudi* are found in southern Africa (Csorba et al., 2003; Hutson et al., 2019). Due to the ambiguous position of *R. darlingi* either in the *ferrumequinum* (morphology) or *fumigatus* (molecular) group (Hutson et al., 2019), we here retain it as a distinct species group. Although having a tropical forest center of origin, four of the groups here studied have members occupying both arid and mesic zones across the Escarpment, the *capensis* group, the *ferrumequinum* group, the *darlingi* group, and the *fumigatus* group.

Two other genera of bats (*Cistugo*, *Laephotis*) have arid and mesic relatives in southern Africa. Southern African-endemic wing-gland bats (Family Cistugidae) comprise two closely related species, *Cistugo seabrae* (arid, western Escarpment) and *C. lesueuri* (mesic, CFB and eastern Escarpment; Monadjem et al., 2020; Stadelmann et al., 2007). Long-eared bats within the genus *Laephotis* (Family Vespertilionidae), comprise central African Miombo savanna (*L. angolensis* including *L. botswanae s.s*), arid (*L. namibensis* s.s.), Mediterranean CFB (*L.* cf. *namibensis*), temperate-montane Maloti Drakensberg (*L.* cf. *wintoni*, *L.* cf. *botswanae)*, and East African temperate-montane (*L. wintoni* s.s.) species and lineages. Some of these (*L.* cf. *namibensis*, *L.* cf. *botswanae*, and *L.* cf. *wintoni*) have not been formally described but represent distinct molecular (cyt-b) and/or morphological entities (Monadjem et al., 2021; Taylor et al., 2022).

Based on our combined biogeographical, molecular, and phenotypic data, we predicted that Pleistocene climate fluctuations superimposed on the geomorphology of the Escarpment would explain vicariance patterns, introgression events, and adaptive differences between lineages within species currently occurring widely on arid and temperate mountains, while Pliocene forest contraction would explain both dispersal pathways and vicariance patterns between older species pairs from arid and temperate mountains, especially in *Rhinolophus* clades known to have tropical origins and older crown diversification dates. Due to the scarcity of nuclear (nuc) DNA sequences for our study taxa and region, our phylogeographic study was based on mitochondrial (mt) DNA (cyt-b) sequences. Recent studies in African horseshoe bats have shown that the two approaches are complementary, with mtDNA being faster coalescing, revealing finer-scale intraspecific phylogeographic patterns, and nucDNA being more reliable for species and higher taxa recognition (Benda et al., 2024; Demos et al., 2019; Uvizl et al., 2024). Discordance between mtDNA and nucDNA arises due to mtDNA introgression between species, a relative frequency occurrence in the evolution of bats. We show how, in the absence of nucDNA sequences, morphological characters in combination with mtDNA sequence data can identify potential introgression events. We identify one such introgression event between *R. damarensis* and the newly described *R. cervenyi*, which has been independently corroborated by a comparison of mtDNA and nucDNA from the same taxa (Benda et al., 2024).

2 | MATERIALS AND METHODS

2.1 | Data collection and acoustic recording

For the six selected species groups, we compiled acoustic parameters from echolocation calls from the literature and new acoustic recordings obtained during this study (211 new call sequences; see details below). We compiled cyt-b sequences from GenBank (https://www.ncbi.nlm.nih.gov/nuccore), and we sequenced tissue samples from six newly captured individuals or museum specimens, comprising four species from the KZN and Free State provinces of South Africa (see below). We conducted craniometric and bacular (penis bone) measurements from museum and private collections (54 bacula and 424 skulls; see details below; Table S3).

For *R. cervenyi* and *R. acrotis*, we conducted passive acoustic monitoring of echolocation calls using Song Meter (SM) Mini-4 bat detectors (Wildlife Acoustics, USA), deployed in the eastern Free State province at five apple farms between Warden and Fouriesburg, in the Golden Gate Highlands National Park and the Witsieshoek Community Conservation Area (99 call sequences). With Echo Meter-3 (EM3) bat detectors (Wildlife Acoustics, USA), we also actively recorded handheld, flight cage-flown or release calls from individuals of *R. cervenyi* (48 call sequences) and *C. lesueuri* ($n = 64$ call sequences) captured at Schaapplaats Farm near Clarens using mistnets of 6, 9, and 12 m lengths (Avinet, USA) and a two-bank harp trap (Faunatech, Australia). Selected call sequences of high signal-to-noise ratio from both passive and active recordings were analyzed with Kaleidoscope Pro v. 4.5.5 (Wildlife Acoustics, USA). For each call sequence, we obtained the number of pulses, characteristic (Fc), minimum (Fmin), and maximum (Fmax) frequencies (kHz) and call duration (ms).

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After obtaining acoustic recordings and standard external measurements, two specimens were then sacrificed using cervical dislocation, pectoral muscle samples were dissected and stored in DNA/RNA Shield and these specimens were prepared in formalin and donated to the mammal collections of the National Museum, Bloemfontein, and the Durban Natural Science Museum. Collection of bats for the project was allowed with the permission of the Animal Ethics (Clearance no.: UFS-AED2021/0029/21) and Biosafety Ethics (Clearance no.: UFS-ESD2021/0233/22) Committees of the University of the Free State and also with permission to do research in terms of Section 20 of the animal diseases act, 1984 (Act No.: 35 OF 1984) from the Department of Agriculture, Land Reform, and Rural Development DALLRD (Reference no.: 12/11/1/4 (2038 RJ)).

Geographical coordinates of relevant GenBank sequences were obtained from Demos et al. (2019), Dool et al. (2016), Taylor et al. (2018, 2022), Curran et al. (2022), and Howard et al. (2022), while coordinates of measured museum specimens were obtained by TCK and PJT. Distribution points of GenBank voucher specimens and museum specimens were plotted using QGIS v. 3.10 (QGIS Development Team, 2023) and NASA's Global Digital Elevation Model (NASA JPL, 2013). Shapefiles of species ranges were downloaded, with permission, from the IUCN Redlist website (https://www.iucnredlist.org/).

2.2 | Biogeographical classification and Maxent distribution modeling

We divided paramontane lineages of 14 recognized taxa into five biome categories (i–v) that partially coincided with both the revised Köppen–Geiger climate classification map (Beck et al., 2018; https://www.gloh2o.org/koppen/) and biomes and ecoregions defined by Dinerstein et al. (2017). Two of these biomes were further subdivided into ecoregions and geographic units (Tables S1 and S2). For the mapping of molecular clades, we used only DNA voucher records or specimen records from which diagnostic characteristics were available.

To obtain projections of climate-change-predicted past and future ranges of species, we used the Maxent program (Phillips et al., 2006), implemented in R version 4.3.3 (R Core Team, 2024) and the packages, "usdm," "dismo," "sp," "raster," "spatialEco," "ncdf4," "tidyr," and "dplyr." A total of 821 occurrence records from 13 of our 14 study taxa (with $n > 5$ occurrence records: two of *Cistugo*, two of *Laephotis*, and nine of *Rhinolophus*) were obtained from Monadjem et al. (2020), supplemented with recent records obtained by AM (unpublished data) and from this study for *R. cervenyi*. The taxonomy followed Monadjem et al. (2020), as updated by Benda et al. (2024), Uvizl et al. (2024) and the results of this study. A total of 19 bioclimatic (Bioclim) variables (downloaded from Worldclim v. 2; Fick & Hijmans, 2017; https://www.worldclim.org/data/cmip6/ at 2.5° resolution) were clipped to a map of southern Africa following the borders in Monadjem et al. (2020). We used the "vif" (variance inflation factor) in package "usdm" to remove highly correlated Bioclim variables, resulting in a final subset of 10 variables used for modeling (bio2, bio3, bio5, bio8, bio9, bio13, bio14, bio15, bio18, bio19). Maps of habitat suitability probabilities were converted into binary maps using the maximum specificity and sensitivity threshold.

To model predicted future climate effects, we downloaded at 2.5° resolution, 19 Bioclim variables for two general circulation models (GCMs), Had-GEM3 and MPI-ESM2, for the worst-case Socioeconomic Pathway (SSP), SSP5-8.5 (ca. RPC 8.5 of IPCC5) from the sixth phase of the Coupled Model Intercomparison Project (CMIP6), reported by the sixth assessment report of Intergovernmental Panel on Climate Change (IPCC6). Since the results were very similar for both GCM's, we present here only the results from Had-GEM3. To model past distributions from the LGM, we downloaded Bioclim variables from the MIROC-ESM GCM of the CPIM5, which were analyzed as described above.

2.3 | Molecular sequences

Cyt-b sequences were compiled from GenBank and obtained for newly collected samples of pectoral muscle stored in DNA/RNA Shield of *R. cervenyi* and *C. lesueuri* from the eastern Free State Province, as well as from skull scrapings of one museum specimen (DM 7504) of *C. lesueuri* from the KwaZulu-Natal Drakensberg. We followed Taylor et al. (2022) for DNA extraction and cytochrome-b sequencing. DNA was extracted from pectoral muscle tissues using the Zymogen Quick-DNA Miniprep Plus Kit (Irvine, CA, USA). For the *cyt-b* gene amplification, we prepared 1×DreamTaq buffer (10×, Thermo Fisher Scientific, Waltham, MA, USA), 2 μL *cyt-b*-LGL 765 forward primer (10 mM, Metabion International AG, Planegg, Germany) (5′-GAA AAA CCA YCG TTG TWA TTC AAC T-3′), 2 μL *cyt-b*-LGL 766 reverse primer (5′-GTT TAA TTA GAA TYT YAG CTT TGG G-3′) (10 mM, Metabion International) (Bickham et al., 1995), 1 μL dNTPs mix (10 mM, Thermo Scientific), 2 μL MgCl2 (25 mM, Thermo Scientific), 0.25 μL DreamTaq polymerase (5 U/μL, Thermo Scientific), and nuclease-free water (Ambion, Foster City, CA, USA) to a final volume of 45 μL. A volume of 5 μL extracted DNA was added to the reaction and incubated in a SimpliAmp automated thermal cycler (Thermo Fisher Scientific) at 94°C for 2 min, followed by 40 cycles of 94°C for 30 s, 42°C for 30 s, and 72°C for 90 s, with a final extension step of 72°C for 10 min.

New cyt-b sequences from this study were added to the GenBank database under the following GenBank accession numbers: OR594340 (Field no.: "PT2021-18," *Rhinolophus cervenyi*) and OR594341 (Field no.: "PT2021-19," *Cistugo lesueuri*) from Schaapplaats Farm in the Free State Province, from *R. acrotis* (GenBank no.: PP706136 = "Bat53"), *R. swinnyi* (GenBank no.: PP706135 = "Bat52") and *R. cervenyi* (GenBank no.: PP706137 = "Bat6") from Wakefield Farm in KwaZulu-Natal Province (Howard et al., 2022), and PP101597 from *C. lesueuri* from Kamberg in KwaZulu-Natal Province (Durban Natural Science Museum accession no.: "DM 7504").

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2.4 | Phylogenetic analyses

Separate analyses were performed on three cyt-b datasets, each focused on southern African taxa with east and west African sequences and outgroups added for reference: (i) Rhinolophidae (horseshoe bats) from the *R. capensis*, *R. damarensis*, *R. ferrumequinum*, and *R. fumigatus* groups, with Hipposideridae (*Hipposideros ruber*) as outgroup; (ii) Cistugidae (wing-gland bats), with Vespertilionidae (*Myotis myotis*) as outgroup, and (iii) long-eared bats of the genus *Laephotis* of the family Vespertilionidae from southern and eastern Africa, with Miniopteridae (*Miniopterus fraterculus*) as outgroup. We analyzed 54 sequences and 773 base pairs in total for Rhinolophidae, 10 sequences and 646 base pairs for Cistugidae (except for DM 7504 for which only 291 base pairs were available) and 29 sequences and 646 base pairs for Vespertilionidae. FASTA files of all sequence data files for *Rhinolophus*, *Cistugo*, and *Laephotis* are provided in Datasets S1, S2, and S3, respectively.

Sequences were aligned using MAFFT v.7 (Katoh & Standley, 2013) to generate a multiple sequence alignment (MSA) using default parameters. The MSA ensures proper alignment of homologous positions across sequences. We used the Basic Local Alignment Search Tool (BLAST) of NCBI GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to perform searches of nucleotide sequences on NCBI GenBank mostly closely matching our new cyt-b sequences. To determine the best-fit substitution model for the aligned sequences, ModelFinder (−m MFP) option (Kalyaanamoorthy et al., 2017) within IQ-TREE v. 2.0.3 (Minh et al., 2020; Nguyen et al., 2015) was employed. ModelFinder utilizes the Bayesian information criterion (BIC) to select the most appropriate substitution model that best describes the evolutionary process of the sequences. For *Cistugo*, the best-fit model according to BIC was TIM2 + F + I + G4. For *Laephotis* the best-fit model according to BIC was TN + F + I + G4. For *Rhinolophus*, the best-fit model according to BIC was TPM2u + F + G4. The phylogenetic tree was inferred using the maximum likelihood (ML) method implemented in IQ-TREE v. 2.0.3 (Minh et al., 2020; Nguyen et al., 2015). The previously selected substitution model was applied during tree construction. Branch support for the ML analysis was assessed with 1000 SH-like approximate likelihood ratio test (SH-aLRT) replicates (Guindon et al., 2010), aBayes posterior probability (Anisimova et al., 2011), and 1000 ultra-fast bootstrap (UFBS) replicates (Hoang et al., 2018; Quang et al., 2014). Node support values, SH-aLRT, aBayes, and UFBS were considered strong when higher than 80%, 0.7, and 95%, respectively (Anisimova et al., 2011; Guindon et al., 2010; Hoang et al., 2018). The resulting phylogenetic tree, along with the associated support values, was visualized using FigTree v 1.4.4 (Rambaut, 2018) to inspect the inferred relationships among the taxa. For each dataset, MEGA program v. 11 (Tamura et al., 2021) was used to calculate uncorrected P-divergences between and within species.

For dating purposes, phylogenetic trees were also inferred using Bayesian analysis as implemented in BEAST v.1.10.4 (Drummond et al., 2018). We used subsets of each of the above datasets with representatives of the key well-supported clades identified by ML (30 sequences for Rhinolophidae, 16 for Cistigudae, and 19 for Vespertilionidae). We used an uncorrelated relaxed molecular clock and the tree prior was set to "Speciation: calibrated Yule." Bayesian Markov Chain Monte Carlo (MCMC) chains were set to 25 million iterations, sampling every 1000 steps for optimal ESS scores and four independent runs were performed. Output log files were visually inspected to check for convergence in parameters using Tracer v.1.7.2 software (Rambaut et al., 2021). The effective sample size (ESS) values were always >500 for all parameters estimated, suggesting that the MCMC runs had reached stationarity. LogCombiner v.1.10 (Rambaut & Drummond, 2018b), was used to combine log and tree files for all four runs for each dataset. The final phylogenies were then constructed in TreeAnnotator v.1.10.4 (Rambaut & Drummond, 2018a) with a burn-in value of 10%. For visualization and manipulation of the phylogenetic trees, FigTree v.1.4.4 software was used.

2.5 | Molecular dating

We estimated the time to the most recent common ancestor (TMRCA) for clades of interest using BEAST v1.10.4 (Drummond et al., 2012, 2018) as described above. We used different fossil calibration points for the three different analyses. As shown clearly by Morales et al. (2019), the choice of fossil calibration dates can result in widely varying date estimates. Taxonomic controversy about the generic affiliation of fossil taxa, for example, in the genus *Myotis*, can also result in widely varying calibration points. We used a definition of "true" *Myotis* provided by Morales et al. (2019), which defines the *mystacinus* clade as sister to the group, and we therefore included a sequence of *M. mystacinus* in our sample of *Myotis* species for the separate analyses of *Cistugo* and *Laephotis*. Following Jacobs et al. (2013), Foley et al. (2015), Amador et al. (2018), and Dool et al. (2016), the BEAST trees for Rhinolophidae were calibrated using normal tree priors with (i) an upper limit of 5.3 Ma and a lower limit of 1.8 Ma for the sister species split between *R. ferrumequinum* and *R. acrotis* based on fossil dates for *R. ferrumequinum*, described from deposits in Poland (Woloszyn, 1987), (ii) an upper limit of 18.74 Ma and lower limit 15.07 Ma for the crown age of Rhinolophidae (Amador et al., 2018; Dool et al., 2016; Foley et al., 2015), and (iii) an upper limit of 55 Ma and a lower limit of 37 Ma for the split between the Rhinolophidae and the Hipposideridae (Amador et al., 2018; Eick et al., 2005; Teeling et al., 2005). Following Stadelmann et al. (2007), Ruedi et al. (2013), Amador et al. (2018) and Morales et al. (2019), BEAST trees of southern African *Cistugo* species as well as southern African *Laephotis* used the same calibration points with normal priors for (i) 28–37 Ma for *Myotis-Murina-Kerivoula* (Morales et al., 2019; Ruedi

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et al., 2013), (ii) 20–34 Ma for the crown date of *Myotis* assuming a conservative Oligocene radiation for "true" *Myotis* (Morales et al., 2019), and (iii) 3.6–11.2 Ma for the node *M. bechsteinii-daubentonii* (Morales et al., 2019; Stadelmann et al., 2007). In addition to these dates, following the recent dated phylogeny of Amador et al. (2018), we constrained trees to the estimated divergence times for Cistugidae-Vespertilionidae (43.2 Ma), for the Cistugidae analysis, and Miniopteridae-Vespertilionidae (47.8 Ma) for the *Laephotis* analysis. In both cases, we used normal priors with varying SDs from 1 to 2 in different runs. Estimated divergence times did not vary substantially with varying SDs for nodes of interest in this study. We similarly found that nodes of interest were robust when using alternative priors such as the lognormal prior, although the latter often produced high intervals or extreme median values of node dates. Since the fossil calibrations we used did not assume a minimum age having a higher probability than older dates (i.e., a right-tailed lognormal distribution) we preferred the normal distribution which also resulted in higher ESS values in general and better convergence of parameters between runs.

2.6 | Craniometric and bacular morphological variation

TCK measured 13 craniometric variables in 273 skulls of *Rhinolophus* (following Csorba et al., 2003; Jacobs et al., 2013 and Curran et al., 2022) and 17 variables in 65 skulls of *Laephotis* (following Kearney & Seamark, 2005). JW measured 17 variables in 86 skulls of *Cistugo*. Skulls were measured from 12 museum collections, as well as privately collected specimens (Table S3). TCK measured nine variables in 54 prepared bacula (penis bones) of 11 *Rhinolophus* taxa recognized by this study. Lateral, dorsal, and ventral photographs were obtained for representative bacula of each of the 11 species. Because previous studies found no evidence for sexual dimorphism in craniometric variables, in *Rhinolophus* (Taylor et al., 2018) and African pipistrelloid bats (Taylor et al., 2022), we combined data for the different sexes. The degree of molar tooth wear ("age class") was noted in each skull. To minimize variation due to age differences, juveniles, having unfused phalangeal epiphyses, and/or unworn molars, were excluded. Landmarks for different craniometric measurements are illustrated and described in Figure S2.

Principal component analysis (PCA) was performed on six datasets comprising nine to 17 log-transformed cranial variables for the six selected species-complexes, four within *Rhinolophus* and one each for *Laephotis* and *Cistugo*. In all cases, PCA was performed on the variable-covariance matrix and no rotation was applied. Since the first two components explained >70% of total variance (except for *R. acrotis*), we plotted biplots of scores from PC1 and 2, as well as tables of variable eigenvector loadings for the first three PCs, using the PAST package (Hammer et al., 2001). Input datafiles for all the above analyses are provided in Datasets S4–S6.

3 | RESULTS

3.1 | Phylogeny and dating

Maximum likelihood trees from cyt-b sequences are shown in Figure 2a–f (selected clades shown in detail for clarity), and Figures S3–S5 (complete ML trees with outgroups), while dated Bayesian trees for the three families are shown in Figures S6–S8. Uncorrected cyt-b P-distances between species and some intraspecific lineages are shown in Tables S4–S6. Node support values and median dates are shown for the major nodes in the ML trees. While the stem dates of all the taxa depicted divergences of the ancestors of Rhinolophidae, Cistugidae, and Vespertilionidae clades in the Eocene (>40 Ma), the crown dates for diversification within the three selected families varied considerably from 16.8 (95% HPD 14.9–18.69) Ma for Rhinolophidae (Figure S6), 1.42 (0.72–2.48) Ma for *Cistugo* (Figure S7), 3.46 (0.6–11.9) Ma for *Laephotis*, and 1.46 (0.19–4.43) Ma for the long-eared *Laephotis* clade (Figure S8). The genera *Rhinolophus*, *Cistugo*, and *Laephotis* were all well supported (Figures S2–S4).

3.2 | Phylogeography

Lineages within each of the six bat species groups have distributions that are highly concordant with the boundaries of biomes across different sections of the Escarpment (Figure 2a–f), as detailed below.

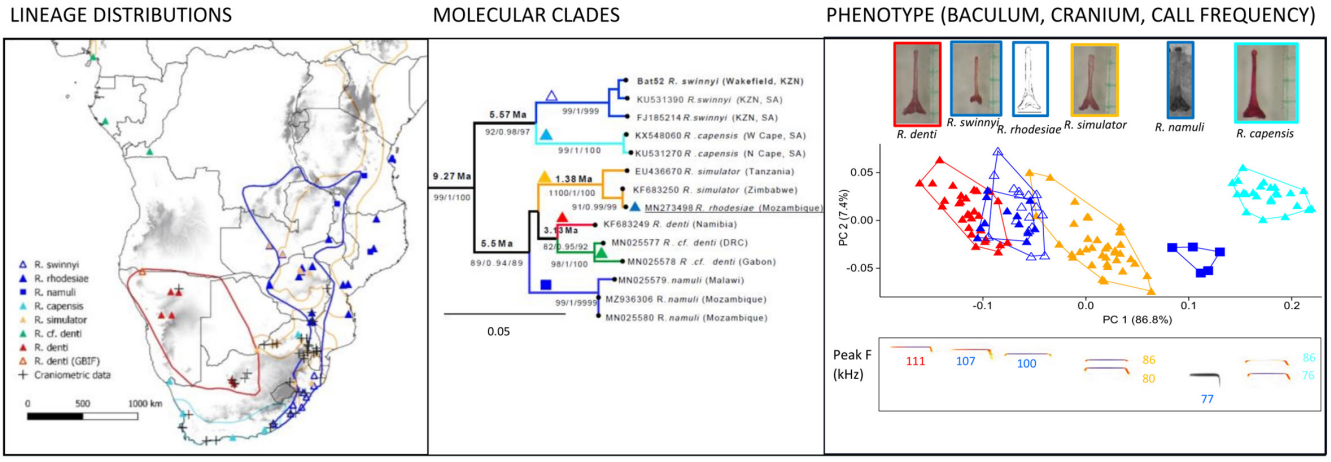
Within the *R. capensis* group, two major clades diverged at 9.27 (6.35–12.78) Ma in the Miocene. Further divergence in each of these clades occurred in the late Pliocene. Firstly, arid-adapted *R. denti* from the western Escarpment diverged from *R.* cf. *denti* from central Africa (W DRC and Gabon) at 3.13 (1.44–4.96) Ma and this combined clade formed an unresolved polychotomy (at Pliocene/Miocene boundary, 5.51 (3.48–8.07) Ma) with *R. rhodesiae* and *R. namuli* (temperate forests in eastern Escarpment, SEAMA and EARS) and *R. simulator* (savannas from northern South Africa to Ethiopia). Secondly, *R. swinnyi* from the eastern slopes of the Maloti-Drakensberg diverged at 5.57 (2.87–8.7) Ma from *R. capensis* from the Fynbos and Succulent Karoo biomes of the CFB and southern Escarpment (Figure 2a).

Within the *R. darlingi* group, *R. cervenyi* from the Maloti-Drakensberg formed a surprising but well-supported monophyletic clade with *R. damarensis* from the semi-arid Nama Karoo biome of the Northern Cape province, separated by a geographic distance of >300 km and an uncorrected P-distance of 0.7% (Figure 2b; Table S4). In turn, this combined Drakensberg + Nama Karoo clade diverged 4.02 (2.23–6.49) Ma from a northern arid clade comprising *R. damarensis* from N Namibia and a sequence from central African tropical forest (W DRC), the latter two sub-clades diverging from each other at 2.4 (1.1–4.14) Ma (Figure 2b; Figures S3 and S6).

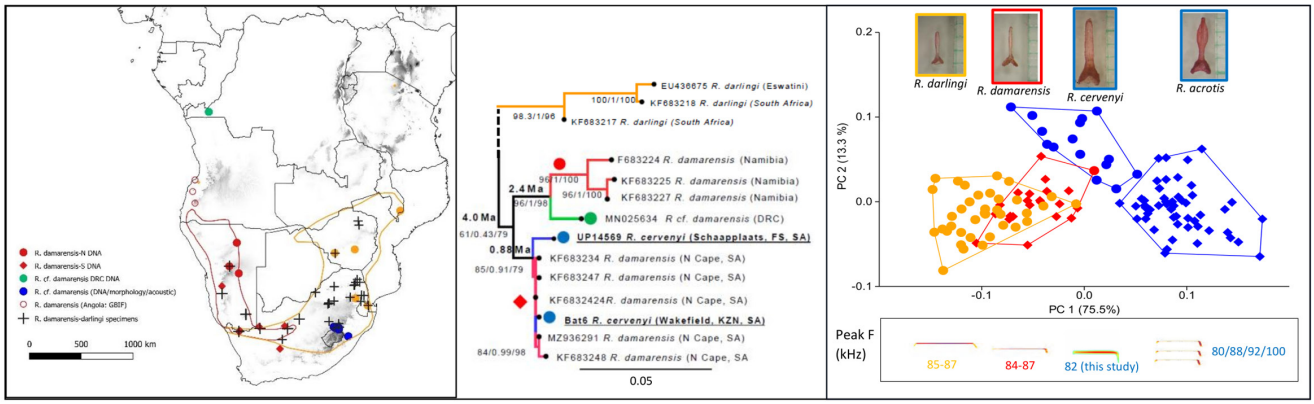
As newly recognized by Uvizl et al. (2024), *R. acrotis* (formerly *R. clivosus*) is broadly distributed throughout southern, central eastern, and northeastern Africa as far north as Ethiopia, comprising, in our

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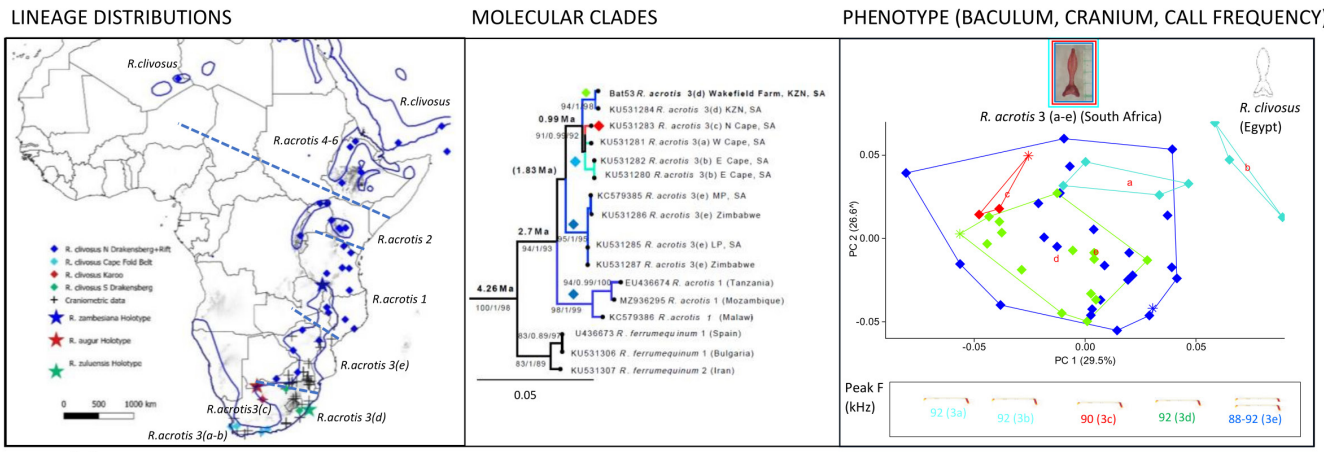
study, three distinct, latitudinally structured mtDNA lineages separated by cyt-b distances of 2.2–3.4% (Figure 2c, Table S4). Its sister species, *R. ferrumequinum* from the Middle East, North Africa and Europe diverged from *R. acrotis* in the Pliocene, about 4.26 (3.03–5.59) Ma (Figure S5). Based on Demos et al. (2019), and our study, two lineages occur in southern Africa, Lineage 3 from the southern and eastern Escarpment and Manica Highlands and Lineage 1 from the SEAMA and EAM. Lineages 2 and 4–6 occur further north in the EARS (Figure 2c; Tables S1 and S2). Based on D-loop sequences, Stoffberg et al. (2012) recognized five lineages in South Africa (a–e) and one in Zimbabwe (e) (Table S1). Our ML (Figure 2c) and BEAST (Figure S5) trees confirmed the geographical patterns above, with Lineages 1 and 3 diverging in the late Pliocene at 2.74 (1.69–3.92) Ma. Within Lineage 3, Lineages (a–d) from arid, Mediterranean, and temperate biomes (southern, central, and western South Africa) and Lineage (e) from highlands of northern South Africa and Zimbabwe formed two well-supported cyt-b clades which diverged 1.83 (1.04–2.79) Ma.



(a) *Rhinolophus capensis* group



(b) *Rhinolophus darlingi* group



(c) *Rhinolophus ferrumequinum* group (in part: Africa)

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FIGURE 2 Distributions (left), maximum likelihood (ML) phylogenetic trees (middle), principal component analysis (PCA) ordination plots from cranial measurements, photographs or drawings of the baculum and sonograms of echolocation calls (right) of selected groups of paramontane southern African bats having ranges categorized as arid (red symbols), Mediterranean (turquoise symbols), temperate-montane (blue), savanna-montane (orange), and tropical rain forest (green; see Table S1 for classification): horseshoe bats (*Rhinolophus*) of the *R. capensis* (a), *R. darlingi* (b), *R. ferrumequinum* (c), *R. fumigatus* (d) groups, wing-gland bats (Family Cistugidae, genus *Cistugo* (e), and long-eared serotine bats of the genus *Laephotis* (f)). Distribution maps were based on IUCN Redlist maps (open polygons), correctly identified vouchers from molecular studies (colored symbols; this study; GenBank; Curran et al., 2022; Demos et al., 2019; Dool et al., 2016; Taylor et al., 2018) and skulls measured in this study (crosses). In a few cases (see legends), GBIF records were indicated for the Angolan range of species. Gray shading indicates elevations over 1200 m a.s.l. Phylogenetic trees are shown for sub-clades (i.e., excluding outgroups) of three separate ML analyses undertaken with IQTREE of *Rhinolophus*, *Cistugo*, and *Laephotis* (Figures S2–S4). Values above nodes (in bold) represent median dates obtained for corresponding nodes from separate BEAST analyses in Figures S5–S7 (see text for details). Node support values for ML trees, obtained by the IQTREE program, are given below the nodes for SH-like approximate likelihood ratio tests (SH-aLRT), aBayes posterior probabilities, and ultra-fast bootstrap values (UFBS) respectively (see text for details). Tip labels marked in bold represent new sequences from this study. Underlined tip labels represent two instances of mtDNA introgression where morphologically distinct taxa from different biomes have near-identical cyt-b sequences. Species ranges of echolocation call peak frequencies were obtained from the literature for Rhinolophidae (Adams & Kwiecinski, 2018; Curran et al., 2022; Jacobs et al., 2013; Jacobs et al., 2017; Laverty & Berger, 2020; Monadjem et al., 2020; Mutumi et al., 2016; Odendaal & Jacobs, 2011; Odendaal et al., 2014; Schoeman & Jacobs, 2008), *Cistugo* (Monadjem et al., 2020; Schoeman & Jacobs, 2003, 2008), and long-eared *Laephotis* (Adams & Kwiecinski, 2018; Jacobs et al., 2005; Monadjem et al., 2020; Pierce et al., 2011). Bacula photographs and drawings were obtained from this study as well as Benda and Vallo (2012), Taylor et al. (2018), Curran et al. (2022). Abbreviation of South African province names: EC, Eastern Cape; FS, Free State; GP, Gauteng; KZN, KwaZulu-Natal; LP, Limpopo; MP, Mpumalanga; NC, Northern Cape; WC, Western Cape. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Rhinolophus fumigatus is broadly distributed in Africa, with disjunct recognized subspecies from the western Escarpment (arid savanna; *R. f. aethiops*) and eastern Escarpment (mesic savanna woodland; *R. f. fumigatus*; Figure 2d). Following the nomenclature of Demos et al. (2019), three distinct genetic clades occur in southern Africa, "*R. fumigatus-eloquens*" Lineages 4, 6, and 7, which diverged from each other in the late Pliocene 3.27 (1.83–5.07) Ma (Figure 2d; Figures S4 and S7). Lineage 6 corresponds with the arid *R. f. aethiops*, while Lineages 4 and 7 occur sympatrically in Zimbabwe, Mozambique, and Malawi.

Although the stem divergence date of wing-gland bats (Cistugidae) was 42.7 (38.91–46.45) Ma, crown diversification occurred much later in the early Pleistocene, 1.42 (0. 72–2.48) Ma (Figure 2d; Figures S3 and S6). Arid (*C. seabrae*) and Mediterranean (*C. lesueuri* in part) clades formed well-supported (87%/1.0/70%) sister clades, with two new sequences of *C. lesueuri* from the Maloti Drakensberg appearing sister to this clade. A relatively deep divergence ($p = 2.4\%$; 1.11 (0.52–1.95) Ma) within the arid *C. seabrae* clade separated Northern Cape and Namibian sequences. (Figure 2d; Table S5).

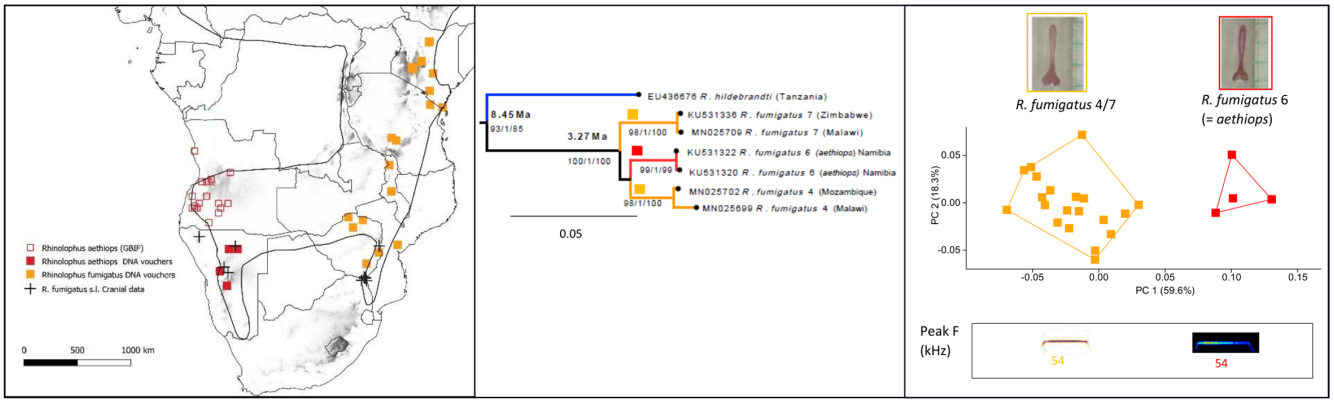
We follow the taxonomy of Taylor et al. (2022) who showed that *L. botswanae* sensu stricto (from Botswana) was synonymous with *L. angolensis*, while specimens of *L. botswanae senso lato* from temperate-paramontane localities in South Africa comprised a uniquely distinct clade, here termed *L.* cf. *botswanae*. From the present ML analysis of cyt-b sequences, long-eared bats formed a well-supported clade comprising sub-clades from temperate-montane (*L. wintoni*, *L.* cf. *botswanae*), savanna (*L. angolensis*), Mediterranean (*L.* cf. *namibensis*), and arid (*L. namibensis*) lineages which diverged from each other 1.46 (0.19–4.43) Ma ($p = 3.0$–4.7%; Table S6; Figure 2f). While savanna, arid, Mediterranean, and one temperate-montane (*L. wintoni*) clade were all well-supported, two *L.* cf. *botswanae* sequences from the Eastern Cape, and Limpopo Provinces of South Africa were sister to this combined clade despite their close genetic similarity to each other ($p = 0.5\%$; Table S6).

3.3 | Phenotypic patterns

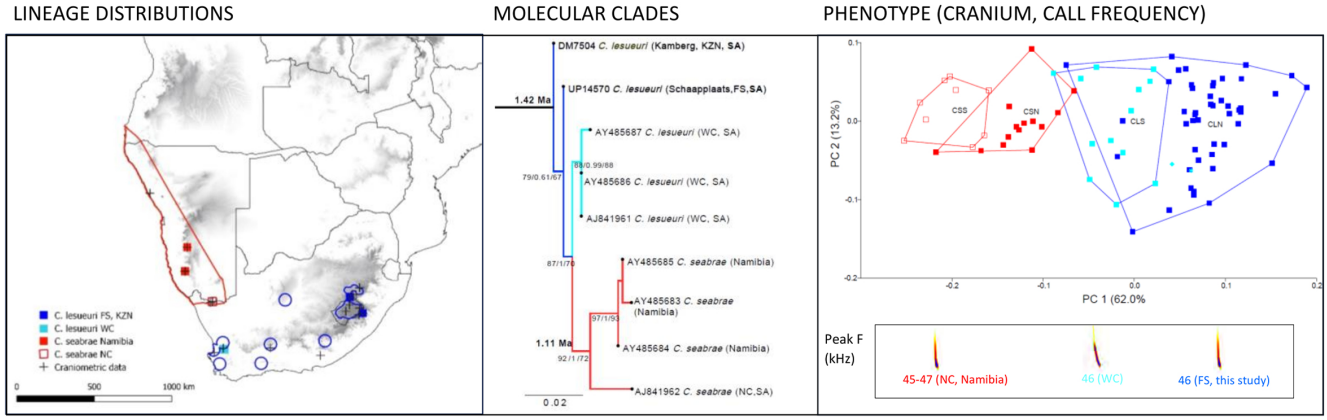
Craniometric relationships are summarized by bivariate plots of PC1 and PC2 scores (Figure 2a–f, right panels) and PC eigenvalues and variable loadings (Tables S7 and S8). Echolocation call parameters for *R. acrotis*, *R. cervenyi*, and *C. lesueuri* from this study are shown in Table S9. Bacular measurements and representative photographs of the baculum of all species in the study are shown in Table S10 and Figure S9, respectively. In *the R. capensis*, *R. darlingi*, and *R. fumigatus* groups, species from different biomes are distinguished from each other in cranial size (PC1 scores; Figure 2a,b,d; Table S7a,b,d). In the *R. capensis* group, cranial size (PC1 scores) is inversely correlated with peak call frequency: the smallest sized taxa (low PC1 scores), *R. denti*, *R. rhodesiae* and *R. swinnyi* have high peak frequencies (100–111 kHz) while the larger sized *R. capensis* and R. *namuli* have lower frequencies of 76–86 kHz and the intermediate-sized *R. simulator* has an intermediate frequency of 80–86 kHz (Figure 2a, right panel). We present new echolocation and baculum size and shape data for the newly described *R. cervenyi*; it has a maximum frequency of 82 kHz from passive recordings, 84 kHz from handheld recordings, and 85 kHz from release calls (Table S9). Its baculum is greatly enlarged and uniquely shaped compared with all other species in our study (Figure S9 (a: f) and S9 (b: a)).

In contrast to the other three older species groups mentioned above, the widespread *R. acrotis* diversified more recently in the late Pliocene/early Pleistocene (after 2.7 Ma) and shows very high intraspecific variability in cranial size and shape (Figure 2c; Table S7c) and

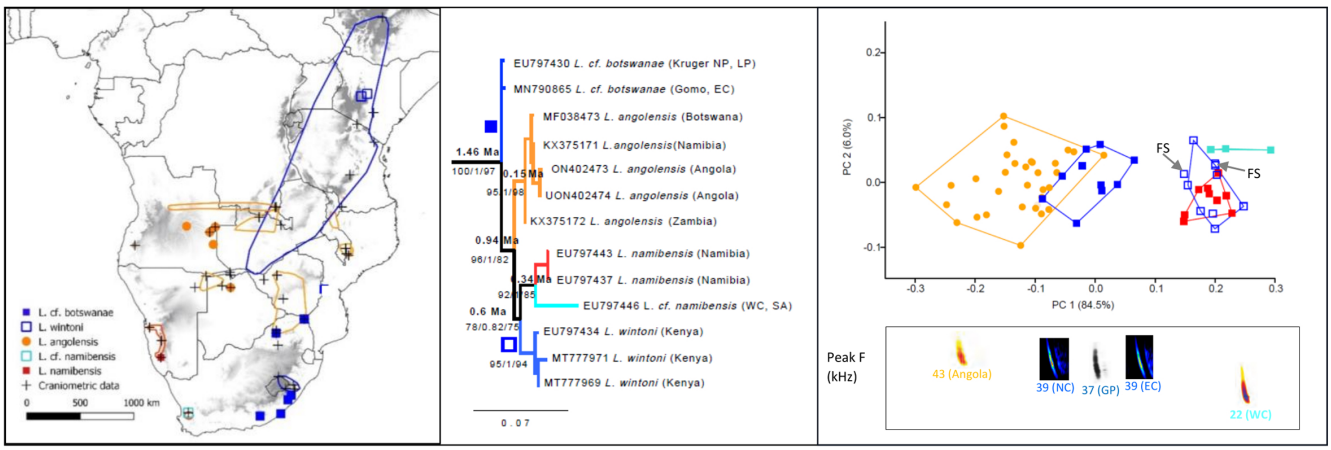
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(d) *Rhinolophus fumigatus* group



(e) Wing gland bats (*Cistugo*)



(f) Long-eared bats (*Laephotis*, in part)

FIGURE 2 (Continued)

echolocation frequency (88–92 kHz in South Africa and Zimbabwe; 81–82 kHz in SEAMA and 100 kHz in Kenya; Figure 2c). However, baculum size and shape is highly uniform within the species, at least for specimens here studied (Figure 2c; Figure S9).

Despite relatively recent diversification in the Pleistocene (1.42 Ma), arid (*C. seabrae*) wing-gland bats are distinctly smaller in skull size (lower PC1 scores) than those from temperate and Mediterranean biomes (*C. lesueuri*) (Figure 2e; Table S8a). With the same crown diversification date (1.46 Ma), two cranial size groups were defined within the long-eared *Laephotis* group, a small-sized group containing savanna and temperate (southern African) taxa and a larger sized group containing arid, temperate (East African) and Mediterranean taxa. Within the former group, temperate *L. cf. botswanae* are slightly larger than savanna *L. angolensis*, but with some overlap between them (Figure 2f; Table S8b).

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3.4 | Distribution models

Model fit for all models was high (Table 1: AUC 0.890–0.997). As determined by percentage contributions and the jackknife test, different combinations of precipitation and temperature variables were important for different species and biomes. Precipitation of the wettest month (Bio13; lowest values more suitable) was the most important environmental variable in the three arid-adapted species, *R. denti*, *R. damarensis* and *C. seabrae*, while mean temperature of the driest quarter (Bio9; intermediate values optimal) was the most important variable in mesic savanna species, *R. darlingi*, *R. simulator*, and *L. angolensis*, as well as in the high-elevation, montane-adapted *R. cervenyi* (lowest values optimal), and precipitation of the driest month (Bio14; intermediate to higher values most suitable) was the most important variable for temperate species like *R. acrotis*, *R. swinnyi*, *R.* cf. *botswanae*.

Maxent past (LGM) models showed that the ranges of temperate, savanna, and Mediterranean species were likely very similar during the LGM compared with present ranges, except in the case of *L.* cf. *botswanae* where populations were more connected across the Drakensberg than is currently the case (Figure 4). On the other hand, species from arid environments had more extensive ranges in the LGM, in *R. denti* which probably occurred much more extensively throughout Botswana and the central regions of South Africa; *R. damarensis* was distributed more extensively in the central highveld of South Africa in closer proximity to the Drakensberg than currently recorded.

Compared with present models, Maxent future (2070) distribution models projected (i) decreases in the ranges of species associated with cold arid, winter-rainfall and temperate climates from higher-lying central African miombo savannas, (ii) increases in species from hot arid climates, but (iii) minimal changes in temperate species associated with the eastern Great Escarpment, possibly due to the buffering effect of mountains to climate change (Figure 4).

4 | DISCUSSION

4.1 | Taxonomic implications

Many new and often cryptic species of Afromontane small mammals have been described in the last three decades (Benda et al., 2024; Curran et al., 2022; Lavrenchenko et al., 2016; Monadjem et al., 2013, 2021; Taylor, Denys, & Cotterill, 2019; Taylor, Kearney, et al., 2019; Uvizl et al., 2024; Voelker et al., 2021). Our analysis identified at least four cryptic species that probably merit formal taxonomic recognition (denoted as "c.f." in Table S2). In fact, one of these was recently formally described as a new species based on specimens and sequences from Lesotho, *R. cervenyi* (Benda et al., 2024). Although Benda et al. (2024) described this mountain species as occurring almost exclusively in Lesotho, based on our genetic, morphometric, and acoustic data (Figure 2b), it is also distributed from the Maloti Drakensberg in the Free State and KwaZulu-Natal provinces and from the Mpumalanga Escarpment, extending also into the KwaZulu-Natal midlands. Specimens of this species were previously misidentified as *R. acrotis* (Benda et al., 2024); however, in our study in the Maloti Drakensberg, *R. acrotis* and *R. cervenyi* had divergent peak frequencies (mean = 92 kHz, 86–94 kHz, $n = 50$; mean = 82.4 kHz, 78–86 kHz, $n = 49$, respectively), and occupied lower (<1900 m) and higher (1700–3060 m) elevations respectively, with limited sympatry at two localities in the Golden Gate Highlands National Park and nearby apple farms (Table S1). As also deduced by Benda et al. (2024), the near-identity of the cyt-b sequences of *R. cervenyi* and the southern clade of *R. damarensis* may be explained by recent mtDNA introgression (see Section 4.2.2).

Similarly, mtDNA introgression explains the genetic proximity of *R. simulator* and *R. rhodesiae* where the ranges of the two species overlap, despite clear-cut species differences in echolocation call frequency (81 and 101 kHz respectively) and external (forearm length), cranial and bacular size and shape which are maintained in sympatry at several localities in South Africa, Zimbabwe and Zambia (Figure 2a; Figure S9; Taylor et al., 2018). Instead, *R. rhodesiae* is indistinguishable in cranial or external morphology from *R. swinnyi* which occurs in the Eastern Cape and southern KwaZulu-Natal, despite deep genetic divergence between them presumably resulting from introgression of the *R. simulator* maternal genome into the former but not the latter. While this situation might argue for the conspecificity of *R. swinnyi* and *R. rhodesiae*, they are easily distinguished on call frequency and baculum size and shape (Figure 2a; Table S3; gracile in *swinnyi* and robust in *rhodesiae*), suggesting that speciation of the two small-sized species preceded introgression of *R. rhodesiae* from the larger sized *R. simulator*. This example underlines the importance of an integrative taxonomic approach (Goodman et al., 2015); considering only molecular evidence without morphological or biogeographical context would erroneously conclude that two (not three) species occur in this group. A precise taxonomic arrangement also allows meaningful analysis of biogeographic affinities between species (see Section 4.2).

Our combined data argue for specific recognition of *R. f. aethiops* from the semi-arid HEAN which is geographically and ecologically disjunct from *R. f. fumigatus* from the eastern Escarpment (Soutpansberg and Manica highlands), EAM, and EARS. The former is significantly larger in cranial size (mean skull length 24.0 mm, 23.7–24.4 mm, $n = 4$) and forearm length (mean 55.2 mm, 51.0–58.0 mm, $n = 16$) than *R. f. fumigatus* from southern and central Africa (mean skull length 22.3 mm, 21.6–23.1 mm, $n = 11$; mean forearm length 51.5 mm, 46.5–58.0 mm, $n = 17$).

Given genetic ($p = 3\%$; Table S6) and biome differences, *L.* cf. *botswanae* from the eastern Maloti Drakensberg and Greater Midlands, LMME, Soutpansberg, and Mozambique may prove to be a species distinct from *L. angolensis* (including *L. botswanae s.s.*) from Miombo highland plateaux of central-south Africa. Similarly, *L* cf. *namibensis* (Mediterranean-temperate) may prove to be species distinct from *L. namibensis* s.s. (arid); their genetic divergence ($p = 3.7\%$) exceeds that found between "good" species such as *L. wintoni* and *L. angolensis* 3.0%; Table S6.

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TABLE 1 Summary of model fit, based on the area under the curve (AUC) of the receiver operating characteristic (ROC) for training data, and the most important bioclimatic variables in past, present, and future (2070) Maxent models of 13 bat species included in this study.

				Top three variables contributing most to model					
Species	*N*	Model	AUC	Rank 1	% contr.	Rank 2	% contr.	Rank 3	% contr.
R. capensis	29	LGM	0.991	Bio19	39.4	Bio8*	26.8	Bio15	13.4
	29	Present	0.95	Bio19**	41.7	Bio8*	27.1	Bio15	17.5
	29	2070	0.991	Bio19	35.6	Bio8*	33.2	Bio13	13.3
R. cervenyi	16	LGM	0.997	Bio9***	57.9	Bio14	23.2	Bio8	7.4
	16	Present	0.997	Bio5*	48.6	Bio9**	33.2	Bio14	13.3
	16	2070	0.997	Bio9***	43.5	Bio14	18.5	Bio18	13.4
R. acrotis	201	LGM	0.905	Bio14*	36.7	Bio8	28.5	Bio3**	18.7
	201	Present	0.90	Bio14	38.0	Bio8	24.2	Bio3**	17.6
	201	2070	0.904	Bio14	36.1	Bio8	28.4	Bio3**	20.2
R. damarensis	40	LGM	0.945	Bio13*	37.9	Bio3**	18.3	Bio2	16.6
	40	Present	0.925	Bio13***	53.6	Bio9	12.9	Bio3	12.3
	40	2070	0.940	Bio13***	59.3	Bio9	17.7	Bio15	6.4
R. darlingi	105	LGM	0.945	Bio3*	28.3	Bio9**	23.9	Bio18	17.2
	105	Present	0.952	Bio9	31.6	Bio14	16.5	Bio2**	16.3
	105	2070	0.953	Bio9***	33.8	Bio14	15.3	Bio2	11.3
R. denti	20	LGM	0.941	Bio13***	59.5	Bio2	19.9	Bio18	11.2
	20	Present	0.941	Bio13***	41.6	Bio2	34.0	Bio18	7.0
	20	2070	0.939	Bio13***	46.5	Bio2	42.0	Bio8	5.2
R. rhodesiae	53	LGM	0.908	Bio13	33.2	Bio3	23.2	Bio2***	22.9
	53	Present	0.899	Bio3	23.8	Bio13	21.8	Bio2	20.6
	53	2070	0.890	Bio13	27.8	Bio3*	22.8	Bio18**	14.2
R. simulator	109	LGM	0.918	Bio9**	31.7	Bio14	22.3	Bio3*	19.1
	109	Present	0.918	Bio9**	34.1	Bio14	17.5	Bio18	16.2
	109	2070	0.919	Bio9***	41.1	Bio14	17.6	Bio18	13.8
R. swinnyi	8	LGM	0.988	Bio14**	76.5	Bio9	17.9	Bio5	4.1
	8	Present	0.995	Bio14*	71.4	Bio5**	21.8	Bio18	3.9
	8	2070	0.996	Bio14*	64.8	Bio5**	29	Bio18	3.6
C. lesueuri	20	LGM	0.972	Bio14	45.1	Bio8**	28.8	Bio9*	15.9
	20	Present	0.97	Bio8***	43.8	Bio14	40.3	Bio9	14.4
	20	2070	0.982	Bio8**	39.7	Bio14	39.6	Bio9	14.9
C. seabrae	13	LGM	0.989	Bio18*	43.7	Bio13	34.8	Bio8**	18.7
	13	Present	0.979	Bio13***	84.9	Bio8	6.9	Bio18	2.3
	13	2070	0.979	Bio13***	89.3	Bio8	6.0	Bio2	2.5
L. angolensis	42	LGM	0.912	Bio9*	32	Bio18	23.4	Bio15**	16.1
	42	Present	0.905	Bio9*	34.7	Bio13	25.6	Bio15**	24.8
	42	2070	0.899	Bio9*	26.9	Bio13	21.0	Bio14	16.7
L. cf. *botswanae*	10	LGM	0.982	Bio14***	61.3	Bio9	22.7	Bio18	11.7
	10	Present	0.98	Bio14***	49.0	Bio9	31.2	Bio18	17.1
	10	2070	0.976	Bio14*	35	Bio9**	27.5	Bio5	18.3

Note: *N* refers to the number of occurrence records, and % contr. to the relative percentage contribution of Worldclim2 Bioclimate (Bioclim) variables. Based on the jackknife test of variable importance, the variable marked with a single asterisk is that having the most information on its own while two asterisks indicates the variable having the most information that is not present in other variables and three asterisks indicate when both the above apply.

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4.2 | Biogeographic implications

4.2.1 | Dispersal

Our results suggest that the Escarpment has played an important role in promoting both vicariance and dispersal in bats in different geological periods. Both arms (western and eastern) of the Escarpment have acted as past dispersal routes from the tropics into temperate southern Africa. The western Escarpment (HEAN) was a corridor providing genetic connectivity between two arid-adapted horseshoe bats (*R. denti* and *R. damarensis*) and their central African sister taxa (*R.* cf. *denti* and *R.* cf *damarensis* respectively from western DRC and Gabon). Dispersal from tropical central Africa to southern Africa in these two species pairs predated the isolation and divergence of their most recent common ancestors in the late Pliocene (3.13 Ma: *R. denti*-*R.* cf *denti*) and early Pleistocene (2.4 ma: *R. damarensis*-*R.* cf. *damarensis*). A more recent north–south dispersal along the HEAN is inferred from the hiatus between *L. namibensis* from the Namib Desert and *L.* cf. *namibensis* from the Cedarberg Range of the CFB, more than 600 km apart and 3.7% divergent in cyt-b sequences, indicating a late Pleistocene divergence of 0.34 (HPD 0.01–1.61) Ma. Supporting this central African biogeographic connection, at least five forest-endemic birds from the Angolan highlands have relatives from the Cameroun Volcanic Line in central Africa (Vaz da Silva, 2015), and some Angolan highland rodents have central African affiliations (Krásová et al., 2021).

The eastern Escarpment was an important Pliocene (2.7–4.2 Ma) dispersal route from northeastern Africa into southern Africa for widespread paramontane species such as *R. acrotis* and *R. fumigatus*. In *R. acrotis*, this direction of dispersal is supported by the ML tree showing that the northern lineage from EAMS is sister relative to the successively more derived central and southern African lineages (Figure 2c). This pattern is suggestive of a step-like single radiation of the species from north to south during the early Pleistocene between 2.4 and 1 Ma, with in situ differentiation in successive "steps," as also proposed for samango monkeys, *Cercopithecus albogularis* (Guschanski et al., 2013; Linden et al., 2020), Afromontane musk shrews, *Crocidura* (Dianat et al., 2024), and rodents of the *Lophuromys flavopunctatus* group (Onditi et al., 2021). Repeated south–north radiations along this montane corridor was proposed for the rodent genus *Otomys* (Montgelard et al., 2023).

4.2.2 | Vicariance and historical introgression

Our results identified seven phylogeographic discontinuities, resulting in 29 micro-endemic, mountain-associated lineages from tropical, subtropical, arid, Mediterranean, or temperate biomes (Table S2; Figure 3). The distribution patterns outlined below for bats, from west to east, are supported by those of other Escarpment plant and animal taxa and recognized CPE, of which a few examples are mentioned below.

(i) *HEAN (N-S).* In spite being morphologically similar, a deep divergence ($p = 4.0\%$) separates northern (N Namibia) and southern (S Namibia, N Cape) mtDNA clades of *R. damarensis*. The northern limit of the southern clade is at Maercker's Caves just east of the widest point of the Namib Desert. Since the Namib Desert has remained unchanged since 18 Ma, it is unlikely that vicariance could account for the deep divergence between the two arid clades. A more probable cause for this unusual pattern could be a history of range expansion and introgression between the southern part of *R. damarensis* and the morphologically distinct (but genetically similar) Maloti-Drakensberg species, *R. cervenyi*, as recently confirmed by Benda et al. (2024). The ranges of the two species probably overlapped or at least occurred in closer parapatry (with mtDNA introgression between them) until recently, possibly as recently as the LGM (see Figure 4f). The range of the southern arid clade coincides remarkably with the simulated extent of frost conditions in the LGM compared with the present (Figure 1b), suggesting that this marks the extent of Pleistocene geographical range expansion of the temperate-montane *R. cervenyi* and therefore the overlap (and hence introgression) between the two species, *R. cervenyi* and *R. damarensis* (southern sub-clade). Following this reasoning, if there was no (or limited) historical range overlap or introgression between the two species in N Namibia, the northern clade would then represent the un-introgressed or "true" *R. damarensis* mitochondrial genotype, while the southern arid clade may have been "captured" by *R. cervenyi*. The Pliocene divergence date would then indicate the date of speciation between arid *R. damarensis* and temperate *R. cervenyi*, thus explaining the considerable phenotypic divergence between the two species. The comparatively elongated and much broader baculum of *R. cervenyi* relative to *R. damarensis* suggests a pre-mating reproductive barrier that may have caused asymmetrical mating between the two species during sympatry to promote the spread of the *cervenyi* maternal lineage throughout the range of southern *R. damarensis*, for example, successful pairings between male *damarensis* and female *cervenyi* but not vice versa. The incidence of mtDNA introgression has been shown to be widespread in bats (e.g., Benda et al., 2024; Dool et al., 2016; Taylor et al., 2018) and other small mammals such as rodents (Bryja et al., 2018).

(ii) *HEAN—Karoo (Orange River gap).* Within *C. seabrae*, northern and southern clades diverged in the mid-Pleistocene (ca. 1.43 Ma). The range of the northern clade coincides with the extent of the HEAN from southern Angola to at least as far south in Namibia as Aus, with the southern clade restricted to a small area of the Namaqualand-Richtersveld Ecoregion south of the Orange River in the Northern Cape. The break therefore coincides closely with the lower Orange River valley. The Orange River also marks the boundary between the historical ranges of the Cape Mountain Zebra (*Equus z. zebra*), from the CFB and southern Escarpment (from E Cape to the Karoo) and Hartmann's Mountain Zebra (*E. z. hartmannae*), from the HEAN (Skinner & Chimimba, 2005).

(iii) *Cape Fold Belt (CFB)—Escarpment ("Bedford Gap").* The Bedford Gap in the Eastern Cape province separates the CFB from the southern Escarpment (Sneeuberg and Great Winterberg-Amatola ranges).

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This gap explains vicariance patterns between sister clades of rodents (*Otomys*, *Rhabdomys*) (Ganem et al., 2020; Taylor, Kearney, et al., 2019) and shrews (*Myosorex varius*) (Willows-Munro & Matthee, 2011). It was recognized as one of three "floristic connections" between the CFB and the southern Escarpment by Clark, Barker, and Mucina (2011a), Clark, Barker, McMaster, and Mucina (2011). In our study, the Bedford Gap explains one Pliocene and two Pleistocene vicariance events in bats. It coincides with the late Pliocene (5.7 Ma) split between the sister species, *R. capensis*, a predominantly CFB species, and *R. swinnyi*, a temperate forest species from the southeastern and eastern Escarpment (Moir et al., 2020, Monadjem et al., 2020; Figure 2a). Forests were continuously present in the Western Cape and southern Namaqualand up to 5.3 Ma (late Miocene), after which they retreated to major river valleys due to the onset of more arid conditions in central Africa (Scott et al., 1997). This may explain the late Miocene speciation of *R. capensis* from *R. swinnyi*. The same scenario was used to explain the presence of a relic species of Clivia (*Clivia mirabilis*) in the Hantam–Roggeveld mountains of the southwest Escarpment, >800 km from its closest relative, *C. nobilis* from coastal and scarp forests in the Eastern Cape (Dixon, 2011; Rourke, 2002).

A more recent mid-Pleistocene vicariance event (0.99 Ma) separated *R. acrotis* from the CFB (Lineages 3b-c) from Lineage 3d from the southeastern and eastern Escarpment (Stoffberg et al., 2012; Table S2; Figure 2d; Figure S5). Similarly, based on our BEAST tree (though not ML tree), lineages of *C. lesueuri* from the CFB and eastern Escarpment (western slopes of Maloti Drakensberg) diverged in the mid-Pleistocene at 0.52 Ma (Figure S6).

Many botanical examples document biogeographical links between the CFB and different sections of the southern Escarpment (Clark et al., 2011a, 2011b, 2011c; Clark, Barker, McMaster, and Mucina (2011); Galley et al., 2007; Weimarck, 1941). For example, although similar floristically, the Hantam–Roggeveld Centre of Plant Endemism (southwestern Escarpment) differs in composition from the CFB located 80 km to the south (across the Tanqua Karoo semi-desert) in the absence of classical restioid, proteoid, and ericoid Fynbos elements from the former (Clark, Barker, & Mucina, 2011a, 2011b). Based on known sister-group relationships, Clark, Barker, and Mucina (2011a) reviewed several additional examples which support biogeographic links between plant taxa from the CFB, the southern Escarpment, and the eastern Escarpment (Drakensberg CPE). Notably, eight CFR-endemic species or subspecies occur not only in the CFB, but also from the adjacent, semi-arid, Namaqualand and Richtersveld Ecoregion of Dinerstein et al. (2017). These taxa have sister groups from either the southwestern or southeastern sections of the southern Escarpment and/or the eastern Escarpment (Table S11).

The close association between the CFB and arid Namaqualand elements in plants is echoed by the distribution of *R. capensis* which occurs throughout the CFB and Namaqualand (Figure 2a). By contrast, *R. acrotis* occurs throughout the CFB and eastern Escarpment, but is not found on the southern or western Escarpment or Namaqualand. In this case, isolated populations of the species from arid inselbergs of the Nama Karoo (north of the Escarpment) are likely to be Pleistocene refugia that were connected to the central plateau of South Africa during a previous hypothermal period (see (iv) below).

(iv) *Karoo-Drakensberg*. In the absence of any obvious physical barriers between the limits of the western Maloti Drakensberg and Nama Karoo, vegetation barriers mediated by Pleistocene cyclical climatic and habitat changes ("species pumps") have been advanced to explain the origin of arid South African vertebrate species (e.g., Matthee & Flemming, 2002; Outlaw et al., 2007; Swart et al., 2009). As argued above, such a late Pleistocene or Holocene species pump can explain repeated range expansion-contraction of temperate *R. cervenyi* and its mtDNA introgression with arid *R. damarensis*. Similarly, the outlying Nama Karoo Lineage (3c) of *R. acrotis* argues for historical connections between Nama Karoo refugia, the Maloti Drakensberg and CFB lineages (at ca. 0.99 Ma) associated with the range expansion and contraction during glacial and inter-glacial peaks, respectively (Figures 1b and 2c). A similar pattern is found in striped mice (*Rhabdomys*) where species associated with the Nama Karoo (*R. bechuanae*) and Grassland (*R. dilectus*) biomes form contact zones in the central Free State and Gauteng provinces (Ganem et al., 2020). Several bird species pairs follow this biogeographical pattern, for example, the western Karoo (*Turdus smithi*) and eastern Olive (*T. olivaceous*) Thrushes, (Bowie et al., 2004), the Yellow (*Crithagra flaviventris*) and Forest (*C. scotops*) Canaries, the Karoo (*Prinia maculosa*) and Drakensberg (*P. hypoxantha*) Prinias and Ludwig's (*Neotis ludwigi*) and Stanley's (*N. denhami stanleyi*) Bustards (Sinclair et al., 2020). Partly sympatric sister species of red rock hares are associated with the eastern and southern Escarpment (*Pronolagus saundersiae*) and the northern Karoo (*P. rupestris*) (Matthee & Robinson, 1996).

(v) *W-E Drakensberg*. Although the highest Maloti Drakensberg peaks do not appear to separate any sister species of paramontane bats, they nevertheless appear to be an important barrier limiting the eastward or westward range of species found only on the western (*L.* cf. *wintoni*, *C. lesueuri*) or eastern (*R.* cf. *swinnyi*, *L.* cf. *botswanae*) aspects of this mountain range respectively. Those species from the moister eastern escarpment of the Drakensberg are forest-associated, while those from the drier (rain shadow) western slopes are typically grassland-associated. Since *R. cervenyi* was recorded from alpine elevations (>3000 m), the high Maloti Drakensberg are not a barrier to this species, and it has been recorded from both the western and eastern aspects. The high Drakensberg is however a barrier to dispersal separating two mtDNA clades of the vlei rat (*Otomys auratus*), one occurring on the South African highveld and western lower slopes of the Drakensberg, and the other on the eastern lower slopes of the Drakensberg. These two clades were estimated to have diverged just after the mid-Pleistocene transition at 0.68 Ma (Taylor et al., 2009).

(vi) Southeastern-northeastern Escarpment (Greater Midlands-LMEE). One species pair exemplifies this pattern; *R. swinnyi* from the eastern Maloti Drakensberg foothills (the southern portion of the Greater Midlands CPE) and *R. rhodesiae* from the central and northern portions of the Greater Midlands CPE, the LMEE and Soutpansberg CPE, Zimbabwe, Zambia, Mozambique, Malawi and Tanzania (Figure 2a; Moir et al., 2020; Taylor et al., 2018). As pointed out in Section 4.1, the two species are most clearly distinguished on their baculum shape (gracile in *swinnyi* and robust in *rhodesiae*),

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and based on this diagnostic character, the two species overlap in the central Greater Midlands (KwaZulu-Natal province) where they are sympatric at one locality. Due to mtDNA introgression from *R. simulator*, it is not possible to date the divergence between the sibling species, or the likely cause of their vicariance. However, it is plausible to speculate that, during Pleistocene glacial conditions, the range of the ancestral temperate-montane species extended from Tanzania in the north to the Eastern Cape province in the south. A subsequent drier and warmer inter-glacial period would have led to local extinction in unsuitable habitats at mid-elevations (e.g., the Greater Midlands which range from 1400 to 1700 m; Carbutt, 2023). Higher mountains such as the Maloti Drakensberg in the south, and the LMEE and other ranges in the north, would have served as refugia within which occurred phenotypic divergence, most notable in baculum shape and echolocation call peak frequency. The ranges of the northern and southern clades would have expanded during a subsequent glacial period, resulting in the current contact zone in the central Greater Midlands. Congruent biogeographic patterns (Greater Midlands-LMME sibling lineage pairs) are known for forest shrews (*Myosorex varius* and *M.* cf. *tenuis*; Taylor et al., 2013), rock hyraxes (Maswanganye et al., 2017), and samango monkey subspecies (*Cercopithecus albogularis shwarzi* and *C. a. erythrarchus*; Linden et al., 2020) as well as within the amaryllid plant genus *Clivia*, with the range of *C. caulescens* corresponding with the LMEE and Soutpansberg, and those of *C. gardeni*, *C. robusta*, and *C. nobilis* corresponding with scarp and coastal forests along the eastern Escarpment.

(vii) *Manica Highlands–SEAMA (Zambezi Valley gap). R. acrotis* Lineages 3 and 1 correspond with this potential barrier (Figure 3). The ranges of *R. rhodesiae* and *R. acrotis* Lineage 3 link the LMEE and Soutpansberg of South

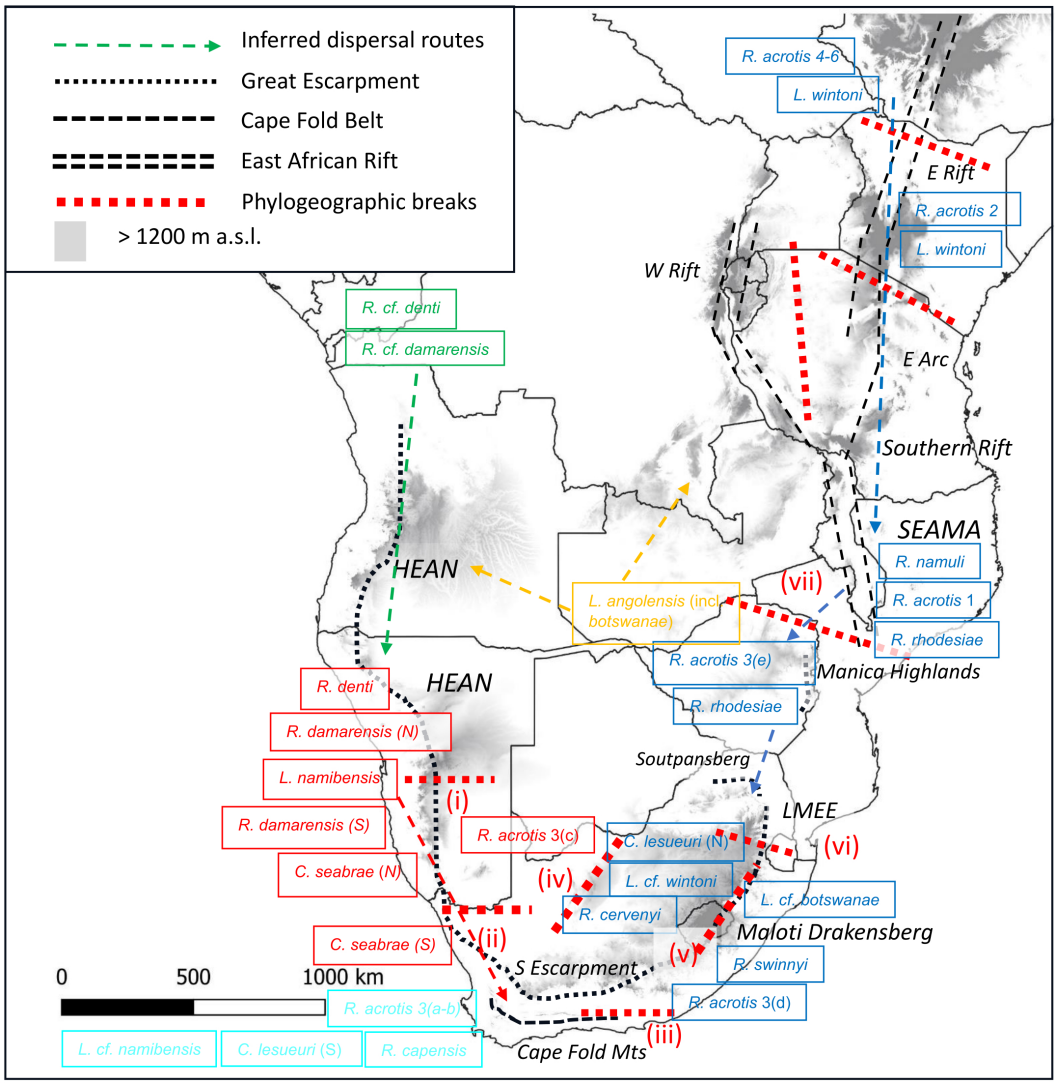
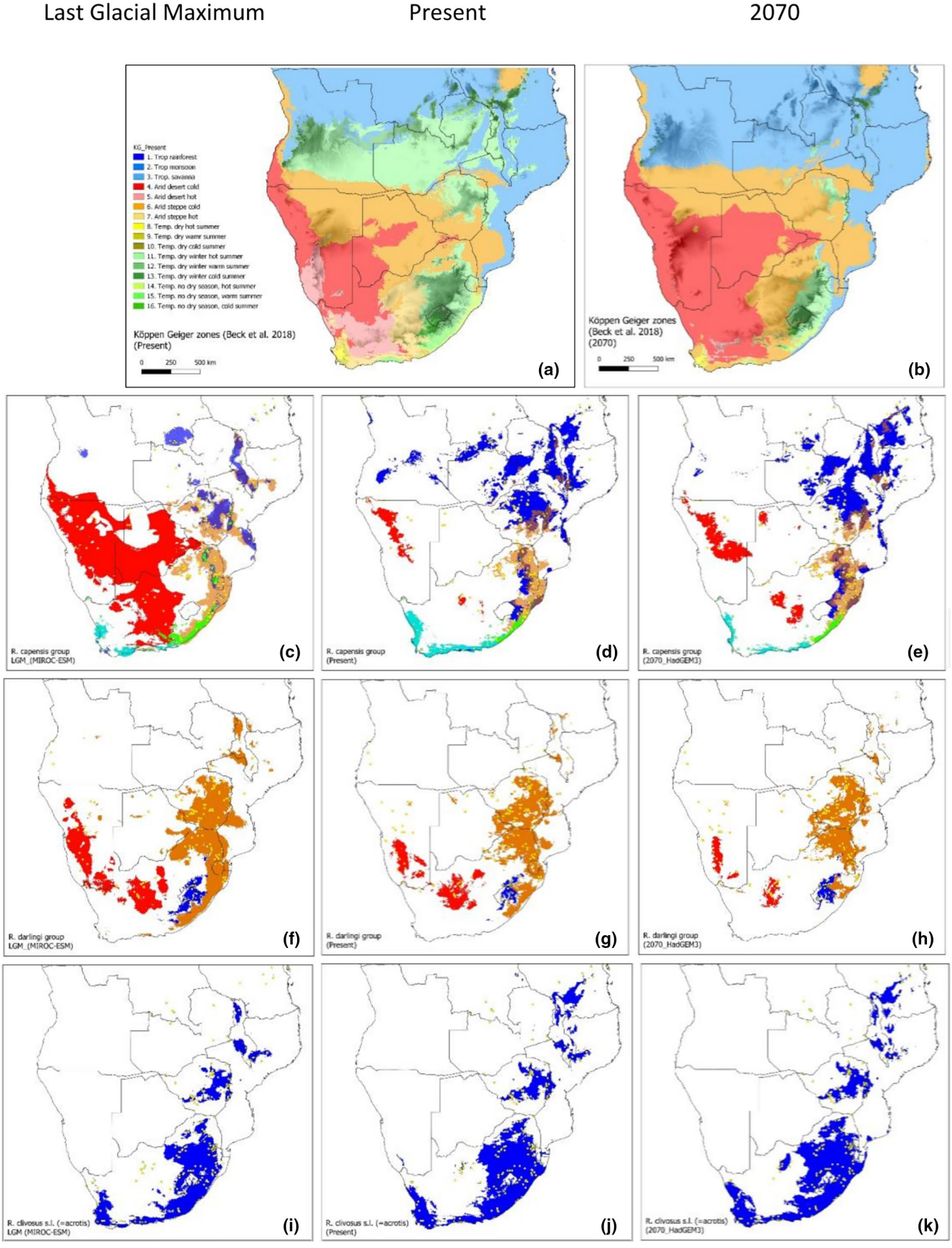


FIGURE 3 Map of southern, central, and eastern Africa showing major geographic features (as in Figure 1a) but with biogeographical barriers elucidated by this study indicated as red dashed lines, labelled as (i) to (vii) (see Discussion), and taxa specific to different ranges indicated according to the predominant biomes (green = tropical; red = arid, turquoise = Mediterranean, blue = temperate, orange = savanna). Note that only one savanna lineage is here indicated for ease of visualization. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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FIGURE 4 Maps of south-central Africa showing the distribution of Köppen–Geiger climate zones for the present (a) and projected future (2070) (b), as well as past (last glacial maximum: left panel), present (right panel), and projected future (2070; right panel) Maxent distribution models for five species groups of bats; *Rhinolophus capensis* group (c–e: green = *R. swinnyi*; blue = *R. rhodesiae*; orange = *R. simulator*; turquoise = *R. capensis*; red = *R. denti*); *R. darlingi* group (f–h: blue = *R. cervenyi*; orange = *R. darlingi*; red = *R. damarensis*), R. *ferruquinum* group, in part (i–k: blue = *R. acrotis*), *Laephotis spp* (l–n: blue = *L.* cf. *botswanae*; orange = *L. angolensis*), *Cistugo spp* (o–q: blue = *C. lesueuri*; red = *C. seabrae*). Details of Maxent models given in text. Ranges of species above indicated by colors corresponding to biomes recognized in this study (Tables S1 and S2) as follows: blue or green = temperate; orange = savanna; turquoise = Mediterranean; red = arid. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

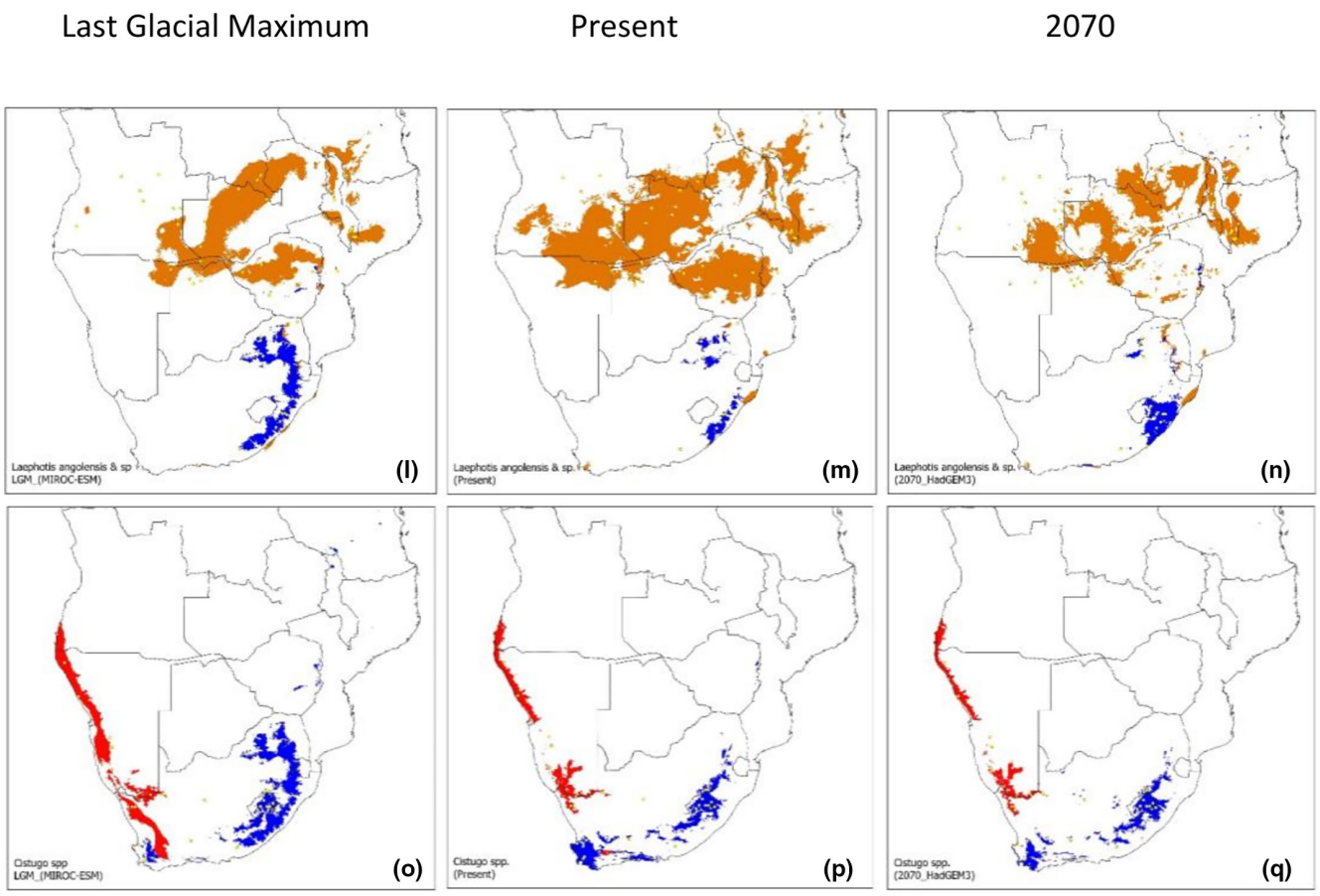


FIGURE 4 (Continued)

Africa with the central and eastern highlands of Zimbabwe, across the arid Limpopo Valley which does not seem to be a barrier to dispersal in bats.

Although not considered in this study, which focuses on the Escarpment, the distribution ranges of *R. acrotis* Lineages 1, 2, and 4–6 (Figure 3) demonstrate additional barriers that can be identified between the E Arc and western (Albertine) and eastern (Kenyan) Rift mountains (see also Nicolas et al., 2020; Taylor et al., 2009) and between the Kenyan Rift and the Ethiopian mountains (see also Dianat et al., 2024 for shrews, and Onditi et al., 2021, Krásová et al., 2022 and Šumbera et al., 2018, for rodents).

4.3 | Conservation implications of climate change

Comparison of current (1980–2016) and future (2071–2100) Köppen–Geiger climate maps (Beck et al., 2018; Figure S1) suggest a reduction in the extent of temperate zones in southern Africa by 2070 at the expense of arid steppes and tropical savanna zones, particularly in medium elevation or isolated highlands such as the central plateaux and northern highlands of South Africa, central highlands of Angola, much of Zambia and central Zimbabwe and isolated inselbergs of the SEAMA. We predicted therefore that species reviewed here having temperate-montane ranges may be severely affected by climate change, particularly in the case of hibernating species of bats where warmer winters could mean a delayed or reduced period of hibernation and/or premature arousal and birth of young during periods of low insect availability. However, data on the physiological capacity of bat hibernators to adapt to seasonal changes due to climate change are currently lacking, especially in the Global South (Festa et al., 2023).

Our Maxent models of 13 paramontane bat species allowed us to test the above prediction. Contrary to our expectations, models did not predict a future reduction by 2070 in the ranges of temperate-montane

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species associated with the higher-elevation Maloti Drakensberg (*R. swinnyi*, *R. cervenyi*, *R. acrotis*, and *L.* cf *botswanae*); instead, their ranges appear remarkably stable over time (Figure 4). We propose that this stability may be at least partly due to the buffering effect of topographic ruggedness and elevational and habitat heterogeneity in high mountains, providing multiple potential refugia in the face of increasingly adverse climate conditions (Pauli & Halloy, 2019). Schoeman et al. (2013) found topographic ruggedness to be the primary driver of species richness in Southern African bats. As expected, bat species with mesic savanna distributions on lower-elevation plateaux and highlands (*L. angolensis*, *R. simulator*, and *R. darlingi*) showed some contraction of their ranges in central Africa by 2070, but not as severe as predicted by the Köppen–Geiger climate models.

5 | CONCLUSIONS

Under past climate change, the Great Escarpment of southern Africa has been an important evolutionary "amphitheater" of bat diversification, acting as both "cradle" (fostering speciation) and "museum" (fostering lineage persistence), and promoting dispersal and vicariance, particularly since the end of the Miocene, 5 Ma, resulting in 29 micro-endemic bat lineages in 14 species from six taxonomically diverse species groups. This high level of endemism and diversity associated with southern African mountains is reflected more generally in plants and animals, providing testable hypotheses for future research. Not only do they house a rich legacy of endemic fauna and flora, but southern African mountains may be important buffers to future climate change, underlining the critical importance of conserving mountain habitats, particularly grasslands which are under increasing anthropogenic threats due to new settlements, conversion to agriculture, increasing fire frequency, overgrazing and rangeland degradation and poor protection status (Carbutt et al., 2017).

AUTHOR CONTRIBUTIONS

Peter J. Taylor: Conceptualization; data curation; formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Teresa C. Kearney:** Data curation; methodology; validation; writing – review and editing. **Vincent Ralph Clark:** Conceptualization; validation; writing – review and editing. **Monday V. Mdluli:** Data curation; methodology; writing – review and editing. **Alexandra Howard:** Data curation; methodology; writing – review and editing. **Wanda Markotter:** Data curation; funding acquisition; project administration; writing – review and editing. **Marike Geldenhuys:** Data curation; methodology; writing – review and editing. **Leigh R. Richards:** Data curation; writing – review and editing. **Andrinajoro R. Rakotoarivelo:** Methodology; writing – review and editing. **Johan Watson:** Data curation; formal analysis; methodology; writing – review and editing. **Julio Balona:** Data curation; validation; writing – review and editing. **Ara Monadjem:** Conceptualization; validation; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw cyt-b sequence data (FASTA files; Datasets S1–S3) and craniometric and specimen data (Excel files; Datasets S4–S7) are openly available on Dryad at https://doi.org/10.5061/dryad.3bk3j9ksc.

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