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To my parents, Mark & Jennifer Cooper, and to Andrea Robinsong, for their constant love and support, and for encouraging me to pursue my dreams.

“In the end we will conserve only what we love, we will love only what we understand, and we will understand only what we are taught.” - *Baba Dioum*

“Life can only be understood backwards; but it must be lived forwards.” - *Søren Kierkegaard*

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CHAPTER 1

ABSTRACT

Evolution and diversification are inextricable intertwined with geography and ecology. The geographic landscape in which a taxon evolves can limit the environments in which it is found or provide opportunities for repeated range contraction and expansion through climate fluctuations. The presence (or absence) of regions with varying levels of climatic stability and the presence (or absence) of major biogeographic boundaries can shape the way in which species diversify or locally go extinct. In tandem with these geographic processes are ecological processes: taxa may interact with co-occurring taxa in the community, and can be limited by biotic barriers (such as disease) or develop specific biotic niches (such as commensalism). In this dissertation, I analyze biogeographic and ecologic drivers of avian evolution from the continental level to individual species interactions. I frame these issues hierarchically, starting with two chapters on large, broad scale patterns that affect not only birds but also mammals, and gradually focusing more and more finely on factors affecting avian systems. The latter part of the dissertation includes three 'case studies' of biogeographic dynamics, with one chapter on community-level dynamics, one on single-lineage diversification dynamics, and one on biogeographic dynamics within lineages that are 'locked' into a mimicry dynamic. Through this research, I demonstrate the ways in with biogeography, ecology, and the overlap between these aspects can drive diversification within avian systems.

CHAPTER 2

INTRODUCTION

2.1 Overview of dissertation

Biological diversification is inextricably intertwined with the ecology of the taxa themselves and the geography in which populations are found [146, 147, 216, 287, 323]. Populations are bounded by biogeographic barriers (*e.g.*, mountain ranges and major rivers) [81, 287, 315] and thus many taxa are likely restricted to portions of their realized niche that are accessible to dispersing individuals both in the present day and through biogeographic history [73, 222, 223, 325]. Barring evolutionary pressures driving ecological diversification (*e.g.*, Eltonian pressures [or lack thereof] driving morphological evolution) [26, 69, 101, 291], the ecological niches of taxa are expected to be conserved through evolutionary time [267, 269, 312], thus reinforcing the biogeographic barriers that bound species.

In geographic space, these dynamics manifest themselves in species' fractured and fragmented distributions. The role of mountains in diversification has been a major focus in biogeographic work, in part because of the propensity for montane regions to contribute to habitat fragmentation through climatic cycling [12, 58, 113, 124, 214, 355]. These dynamics strongly parallel geographic dynamics seen in both temperate regions and tropical lowlands where glaciation and rivers have separated avian populations and led to allopatric diversification [86, 151, 242, 315, 365]. In isolation, populations are then able to accumulate differences in phenotype, morphology, and genotype that subsequently prevent interbreeding when populations come back into contact (*e.g.*, as in *Sclerurus mexicanus*, where multiple populations are vocally distinct and occupying a parapatric mosaic in geographic space) [70, 83, 116, 178, 305].

In the literature, allopatric diversification processes are favored as an explanation for diversification events [216, 284], but diversification events (even wider spread 'radiations' of speciation) can be caused by numerous other factors [314]. Patterns similar to vicariance can also occur via dispersal [282, 380] and from local extinction [279]. Furthermore, parallel patterns of evolution, complex colonization patterns, and character conservatism can complicate mosaics of diversification and cloud relationships between populations [294]. The patterns and processes that drive species diversification are theorized to be similar for many taxa, but robust tests of biogeographic patterns and processes are still lacking in many areas.

Furthermore, species inhabiting similar environments can be constrained by similar biogeographic pressures (*e.g.*, Gloger's Rule) [88, 134, 232] and by their interactions with other co-occurring species, even if those species are only locally sympatric (*e.g.*, via interspecific social dominance mimicry) [277, 278]. These evolutionary pressures can further muddy our understanding of species' diversification and relationships across geographic space, especially when competing evolutionary pressures may be exerted on individual populations.

In this dissertation I explore the ways in which biogeography and ecological pressures shape diversification from the community level to the individual population level. Using these studies at different levels, I am able to demonstrate how geography, ecology, and individual species history influence the diversification of individual species and entire communities.

2.2 Outline of research

I have organized this dissertation hierarchically, such that the subject material herein starts broadly before focusing on more specific examples of diversification and evolution. While ecology and biogeography are often considered separately, these two forces exist in concert and can exist in a spectrum, where differing biotic communities across biogeographic barriers can exert different selection regimes on populations. Throughout all of my chapters, I work towards teasing apart the dynamics between geography, ecology, and time to understand how modern avian communities have evolved.

In Chapter 2, I discuss the ways in which extinction probability alone can lead to the structuring of continental communities. Using theoretical and real data derived from birds and mammals, my co-authors and I demonstrate that reduced extinction rates alone can lead to communities with more phylogenetic dispersion and more phylogenetic diversity. These findings reinforce those of others in tropical regions where large amounts of genetic diversity can accumulate in lineages that are widespread and relatively contiguous in distribution in the modern era [170, 233].

Chapter 3 further investigates shared patterns among biogeographic regions, focusing on species communities across the Afromontane landscape. Using an updated version of a montane species list derived from two previous sources [45, 93], I apply classic and novel clustering techniques to understand biogeographic patterns. I recover many of the same biogeographic regions as other authors, but I shed more light on the ambiguities that exist from complex and conflicting colonization histories, and highlight the importance of connections across previously highlighted biogeographic subregions.

To understand how mountains can lead to parallel patterns of diversification between taxa with drastically different ecologies, I address mitochondrial and nuclear phylogeography in the Lacustrine Rift of Eastern Africa in Chapter 4. Using data collected by my co-authors and historical museum specimens, I show that biogeographic barriers that are geographically similar can have drastically different signatures for many different species, but that severe biogeographic breaks can repeat themselves across many different species' ecologies. However, despite concordances in many areas, these data still highlight how genetic diversity can accumulate within lineages with a history of range fracturing from climatic cycling, especially in the case of *Phylloscopus laetus* [62, 93, 275].

Focusing even more closely within the Afromontane system, Chapter 5 is a single-species case study of *Cinnyris reichenowi* sensu lato across the continent. This species, which has had five subspecies described, is often considered to possess only two major populations in Central Africa (*preussi*) and in East Africa (*reichenowi*). However, by using extensive genetic sampling of historical and modern genetic samples, my co-authors and I are able to demonstrate that a third taxon - *genderuensis* - is valid, and worthy of recognition. Furthermore, we are able to show that there appears to be allopatric diversification occurring within Central Africa between the wet highlands and the mesic plateaus of the interior, though we are unable to conclusively pin this diversification on any particular ecological driver. Lastly, we are able to show that the morphologically near-identical populations of Central and East Africa are best considered separate species.

To understand the ways in which interspecific dynamics and environment drive evolution in species, Chapter 6 takes a closer look at North American black-and-white woodpeckers (*Picoides* sensu lato). In these woodpeckers, size evolves in tandem between the mimic *Dryobates pubescens* and its model, *Leuconotopicus villosus* [69, 276, 278] where the species co-occur across the continent. These two species occur broadly across the North American continent, and only the model (*L. villosus*) exists in regions uninhabited by the mimic (*e.g.*, the Bahamas and south of the Chihuahuan and Sonoran deserts) [31]. Another mimic species (*Dryocopus lineatus*) occurs across multiple biogeographic barriers and thus overlaps with multiple model species in the genus *Campephilus* [31]. By analyzing biogeographic dynamics in these species in conjunction, I am able to show how ecology and environment exert evolutionary pressures within a tightly-linked system of mimicry.

2.3 Important notes

The following important caveats are necessary for understanding my own personal thinking and philosophy behind some of the research contained herein.

2.3.1 Note on species concepts

Species definitions in and of themselves are a contentious issue [283], especially in birds where 'field identifiable' characters are weighted especially heavily [266, 341, 359]. I use the concept of species throughout this manuscript as:

1. species are a useful and necessary unit for defining overall richness, understanding biogeographic patterns, and implementing effective conservation;

2. birds are sexual organisms that experience geneflow between individuals and between populations, unlike organisms such as bacteria, and thus can form individual evolutionary meta-populations evolving together through time; and

3. species are an effective way of understanding biogeographic patterns of diversification and dynamics between different populations.

I do not adhere to any one specific definition for species concepts within this paper, but rather apply a hybrid concept of considering multiple lines of evidence for delineating populations. I acknowledge that speciation and diversification can exist within the presence of gene flow [342, 357], and that small levels of genetic divergence can result in species-level diversification events [228, 343]. Furthermore, I acknowledge that song differences and ecological differences play an important role in separating species, even if their ecologies are similar [23, 205, 219]. I do not, however, adhere to the phylogenetic species concept where every lineage is distinct [18] given the amount of genetic variation that can be maintained and persist across ecological gradients [19, 233].

As mentioned, species limits are a contentious (and sadly often political) issue. In my personal opinion, over-reliance on the biological species concept has stymied research and conservation in the field, and I am one of many ornithologists who is opting for hybrid species concepts that take into account multiple lines of evidence.

2.3.2 Note on definitions, geography, and naming

Many sections of this manuscript assume a certain level of familiarity with global geography, and especially with the geography of Africa. This research focuses on regions with tumultuous geopolitical histories that have had changing borders and possess multiple names for different geographic regions without scientific consensus on how to refer to different regions in the English region. As with many areas, different mountains and regions have multiple different local and regional names, but I try to refer to all places using names commonly found on

English language maps (such as Google maps). Many chapters contain figures providing overviews for geographic regions referenced herein, such as Figures 4.1 & 6.2.

I diverge from convention in some sections of this paper as I try to find better ways to describe regions without imposing colonial terminology. This is especially difficult in regions where local names are not well known in the English literature, or where multiple local names exist and choosing one name would unfairly marginalize other ethnic groups. Given that this is an English language manuscript, I opt for adopting more inclusive English names for different regions when possible. The largest such change contained within this manuscript deals with the Albertine Rift. This region, named after the Queen's consort Prince Albert, often refers to the mountain region spanning several large lakes in the African Rift Valley from Uganda & northern Democratic Republic of the Congo to Zambia & the southern Democratic Republic of the Congo [272]. Here (and in the manuscripts I have submitted for publication), I have coined the new term 'Lacustrine Rift' to refer to this region. This name is more inclusive as it avoids references to colonial etymology and instead focuses on the geographic properties of the region, namely the many large lakes. As we continue to create a more inclusive scientific atmosphere, many colonial names will undoubtedly continue to be replaced.

There are many parallel efforts currently being enacted on bird names as well. Here, I use commonly accepted English names as well as accepted scientific names. However, in all manuscripts where I advocate for the recognition of novel taxa, I avoid English eponyms whenever possible. Eponyms are problematic as they are heavily biased with regards to the people that they honor and with regards to the way they are applied [94]. English names are in-and-of themselves a colonial aspect (and few other languages have global bird name lists; Jacob C. Cooper & Therese Catanach, unpublished), but I try to use names that are descriptive of the birds themselves or of the places they are found in the most neutral terms possible. I acknowledge that I have a long way to go as an individual and as a researcher to improve the inclusivity of the scientific field in many different aspects. I hope that these efforts herein are a step in a positive direction towards creating a more inclusive scientific atmosphere.

2.3.3 Note on research

The research in this dissertation is based entirely upon existing museum collections and freely available data online. Thus, this research exists separate from the museum field work that I was a part of during my PhD tenure. While I did participate in collecting expeditions during the course of my PhD, this work is still in progress and has not been included here. Please see notes on future research at the end of this dissertation for more information. Further information on my field research can be obtained directly from the museums through which work was performed.

CHAPTER 3

CLIMATIC REFUGIA AND REDUCED EXTINCTION CORRELATE WITH UNDERDISPERSION IN MAMMALS AND BIRDS IN AFRICA

3.1 Abstract

Macroevolutionary patterns, often inferred from metrics of community relatedness, are often used to ascertain major evolutionary processes shaping communities. These patterns have been shown to be informative of biogeographic barriers, of habitat suitability and invasibility (especially with regards to environmental filtering), and of regions that function as evolutionary cradles (*i.e.*, sources of diversification) or museums (*i.e.*, regions of reduced extinction). Here, we analysed continental datasets of mammal and bird distributions to identify primary drivers of community evolution on the African continent for mostly-endothermic vertebrates. We find that underdispersion closely correlates with specific ecoregions that have been identified as climatic refugia in the literature, regardless of whether these specific regions have been touted as cradles or museums. Using theoretical models of identical communities that differ only with respect to extinction rates, we find that even small suppressions of extinction rates can result in underdispersed communities, supporting the hypothesis that climatic stability can lead to underdispersion. We posit that large-scale patterns of under- and overdispersion between regions of similar species richness are more reflective of a particular region's extinction potential, and that the very nature of refugia can lead to underdispersion via the steady accumulation of species richness through diversification within the same ecoregion during climatic cycles. Thus, patterns of environmental filtering can be obfuscated by environments that coincide with biogeographic refugia, and considerations of regional biogeographic history are paramount for inferring macroevolutionary processes.

3.2 Introduction

Quantitative assessments of community assemblage and relatedness are often used to assess macroevolutionary patterns of diversification at large spatial scales [81, 128]. On the African continent, range disjunctions shared at the community level have long been studied and interpreted from the perspective of how climate can shape biogeographic patterns [112, 152, 198, 352, 355]. In addition, spatial patterns of species richness and diversification across Africa have led to the identification of evolutionary "cradles", such as mountains, that play a crucial role in building African biodiversity [112, 113]. Similarly, lowland habitats, especially more stable, tropical environments, have been referred to as 'evolutionary museums' – areas in which species diversification is comparatively older and tempered, meaning communities (and species assemblages themselves) have been relatively stable through time [12, 126, 233].

Whether on islands or across continents, local and regional species assemblages are created through a combination of diversification and colonization events, balanced by extinctions [217]. Truly in situ diversification (*i.e.*, wholly sympatric speciation) appears to be relatively rare in nature or requiring specific conditions, with parapatric and allopatric speciation being far more common [78, 322]. Allopatric speciation relies on geographic isolation of species, which only increases the overall species richness when taxa come into secondary contact and their species integrity is maintained [340]. This secondary contact results in the colonization of one or both species into an area that is ecologically suitable but hitherto inaccessible for one or both species. Over evolutionary time, the probability of secondary contact increases, such that on large timescales (i.e., hundreds of thousands or millions of years) increasingly distantly related taxa overlap. Across shorter evolutionary timescales, these divergences can result in evolutionary radiations (e.g., geographic or adaptive radiations) of species that are closely related, patterns that can repeat as evolutionary time increases and a clade's ecological niche becomes more dispersed. Within Afrotherian mammals, for example, multiple evolutionary radiations of different ecologies exist, with more recent radiations existing within some of the differentiated clades (e.g., the Tenrecidae of

Madagascar) [104].

From a meta-community perspective, an appearance of in situ diversification can be explained by diversification events that are limited to the same biome, with limited migration to other biomes [233, 250]. In situ diversification is thus driven primarily by temporary allopatry caused by climatic cycles [275, 355] or fluctuating geographic boundaries such as rivers [81, 248] or, to a lesser extent, by ecological divergence among spatially overlapping populations [26]. These diversification processes create communities that are phylogenetically underdispersed compared to other biomes that are more easily colonizable and thus more likely to possess less related lineages [137]. This process could be accelerated by relatively frequent fragmentation of habitats by environmental cycling, where repeated opportunities for allopatry arise and are subsequently followed by the re-establishment of sympatry or parapatry, thus causing underdispersion to co-occur with temporally unstable environments with low community extinction rates [355]. In other biogeographic regions, underdispersion is often related to 'filtering', wherein only a few lineages are able to colonize and diversify within a specific environment [180, 207]. However, the root cause of the 'filtering' has been called into question, and it is argued that environmental causes for filtering cannot be fully determined even if phylogenetic underdispersion is found to be associated with specific environments [55].

Geographic characteristics affect different lineages in similar ways, such that diversity hotspots for multiple taxonomic groups are frequently spatially coincident [154, 216]. The ways in which climate and geography have influenced evolution (and continue to do so) are further dependent on the evolutionary histories of species and lineages. Like all continents, Africa is biogeographically complex, with northern Africa (namely, the Maghreb) being more closely allied to Eurasia, and with Sub-Saharan Africa being more unique due to its greater biogeographic isolation [77, 173]. Furthermore, Sub-Saharan Africa is associated with several island groups that vary dramatically in their biogeographic histories, with the largest island, Madagascar, possessing endemic incipient evolutionary radiations (e.g., Vangidae [vangas], Bernieridae [tetrakas] and Tenrecidae [tenrecs] and Lemuridae [lemurs]) [104, 291, 376] as well as apparent remnants of animal families that have since gone extinct elsewhere (e.g., Brachypteraciidae [ground-rollers] [201].

The biomes of sub-Saharan Africa can be divided into biogeographic areas. Two major rainforests regions exist, the Upper Guinea forests and the Congo Rainforest (here considered with the connected Lower Guinea Forests), as well as several areas of varying aridity such as the Sahel and the Namib (one of the oldest deserts in the world), and several clusters of geographically disparate but historically connected montane habitats [198]. Diversity for many taxonomic groups peaks in the rugged highlands of the Lacustrine Rift (alternatively known as the Albertine Rift; see Cooper *in review*) where the Congo Rainforest and more xeric East Africa habitats intersect with some of the highest mountains on the continent. Unlike the Andes, which are a highly cohesive mountain chain bisected by deep river valleys and stretching over the breadth of the South American continent, the mountains of Africa are largely clustered and scattered, with the largest geological phenomenon being the Rift Valley. This region, stretching from Malawi and Mozambique to the Red Sea, has resulted in a discontinuous mix of mountains, depressions, and lakes that form an environmental mosaic lacking the uplifted continuity of the Andes or the Himalaya. While it is difficult to assess stability comparatively on continental regions through time, these differences in mountain building across continents may greatly influence comparative climates across continents. During the ice age, the lowland rainforests of Africa were spatially fragmented and restricted in distribution multiple times, creating fractured habitats that were archipelagic in their own right between periods of connectivity [229, 352]. Thus, compared to these fracturing and reconnecting humid lowlands and highlands, many of the xeric and arid habitats of Africa have maintained relative stability, and are known for their remarkable biodiversity (especially for large mammals, larks, and cisticola) [3, 85, 199].

The generation of broad phylogenetic data sets, coupled with documented distribution data in mammals and birds, offers the potential for continental-wide comparisons that can distill the processes that skew phylogenetic dispersion in different habitats and different lineages. To this end, we coupled continent-level phylogenies and presence-absence matrices of mammals and birds in Africa. The archipelagic aspects of many African habitats through evolutionary time present an opportunity to examine the effects of environmental history and geography on patterns of richness and phylogenetic diversity. Specifically, the mix of mountains and lowlands provides an opportunity to determine whether similar biogeographic histories have led wet montane forest and wet lowland rainforest regions to possess similar patterns of community assembly. The geographically large regional environmental fluctuations and disjunctions are well documented, with evidence for a historically savanna-like Sahara extending well into northern Africa [319, 338] and it is possible that there have been repeated disjunctions and reconnections between different lowland rainforest refugia [229, 355].

In order to test how biome stability and biogeographic cycling shapes vertebrate communities in Africa, we performed continental comparisons of richness, mean phylogenetic distance, mean nearest taxon distance, and phylogenetic dispersion for mammals and birds, Africa's most well-known vertebrate groups. We supplement these analyses with a theoretical test of species diversification in similar sized communities with different extinction rates to compare how biogeographic refugia and stability may shape modern communities.

3.3 Methods

All computational analyses were performed in **R** 4.0.4 locally or with **R** 3.6.3 on a server [286], using the package *tidyverse* and its dependencies for general data manipulation [370] and the packages *colourvalues* [67], *ggpubr* [193], *gridExtra* [10], *rasterVis* [264], and *viridis* [125] to assist with plot creation. We performed spatial manipulations of the data using the **R** packages *raster* [160] and *sf* [261] as well as in QGIS 3.18 [281].

3.3.1 Datasets

We processed mammals and birds independently, managed by JCC and NMAC, respectively. We downloaded global range maps for mammals from the IUCN [179] and global range maps for birds from BirdLife International and NatureServe [177]. We generated a presence-absence matrix for both groups using a grid of points that covered Africa and its adjacent offshore islands, sampling at .1° intervals. Subsequently, we downloaded taxonomic trees for mammals and birds from existing studies of global diversity. For mammals, we downloaded a phylogenetic dataset of all African taxa from `http://vertlife.org/phylosubsets/` with 100 trees [346]. For birds, we used the genetic backbone of Jetz *et al.* [186], placing species that lacked genetic information using TACT (Taxonomy Addition for Complete Trees) [59] and the taxonomic data of Jetz *et al.* [186]. This more recent approach for placing species using taxonomic data enables more accurate branch length estimation [59]. We downloaded ecoregion information from the World Wildlife Federation website on 5 March 2021 [253].

3.3.2 Community analyses

We imported our presence-absence matrices into **R**, and calculated α diversity (*i.e.*, richness) as the number of species reported present at each sampling point. For our analyses of MPD, MNTD, and phylogenetic dispersion, we used code from Couch *et al.* [81, 82] supplemented with our own code. We imported phylogenetic trees into **R** using the package *ape* [256]. We obtained values for MPD, MNTD, and phylogenetic diversity (PD) using the commands 'mpd.query', 'mntd.query', and 'pd.query' in the **R** package *PhyloMeasures* [344] applied across our presence-absence matrix and all sampled phylogenetic trees. From these outputs, we obtained average values for each metric from each sampling point from our aforementioned grid, as well as the range of values obtained at each point. We calculated relative dispersion by performing a linear regression using the **R** command 'lm' of mean phylogenetic diversity (from the 'pd.query') and species richness. We then fit a 95% confidence interval around the regression line to define over- or underdispersion. We assigned a value of 0 to points that are underdispersed, 1 to points that are within the confidence interval, and 2 to points that are overdispersed. We compared the counts of points that fall into each of these categories for mammals and birds by way of a χ^2 test called using the **R** function ‘chisq.test’ [286].

For each variable (MPD, MNTD, and phylogenetic diversity), we performed simple linear models of the relationships between variables (using ‘lm’ in **R**) and we obtained the correlation of the variables (using ‘cor’ in **R**) [286]. In order to compare the landscapes of each variable, we converted our sampling points to raster format using the **R** package *raster* [160] and we normalized each variable between 0 and 1 using code adapted for our dataset. We compared rasters using both Schoener’s D and Moran’s I using the command ‘nicheOverlap’ in the **R** package *dismo* [162], and we assessed significance by comparing the values of the real datasets to comparisons of the randomized matrices. Differences between the statistic obtained from actual datasets and the distribution of random datasets was obtained using t-tests in **R** using the command ‘t.test’ [286].

We imported the WWF ecoregions shapefile [374] into **R** using the packages *rgdal* [36], *rgeos* [40], *sp* [41, 262], and *maptools* [39] to compare values for each group across ecoregions, G200 regions (*i.e.*, metaregions of multiple ecoregions), and user-defined metaregions based on ecoregion type (*e.g.*, forest, savanna, etc.) to observe trends. Given that African mammals and birds have different diversification histories, we focused on comparing relative amounts of phylogenetic dispersion between ecoregions. To obtain trends specific to the two classes, we assigned values of 0 for underdispersed, 1 for no significant dispersion, and 2 for overdispersed to each grid cell. We then averaged these values by ecoregion to assess spatially the distribution of over- and underdispersed ecoregions for both classes. We further combined mammal and bird datasets to determine which areas were relatively the most over- and underdispersed for both phylogenetic groups.

3.3.3 Theoretical analyses

To test for the effects of extinction alone on MPD and MNTD, we performed analyses of theoretical communities that are identical in every regard except extinction rate. These theoretical communities all originate from a single source species and then diversify to a predetermined richness, either 100 species or 10 species to mimic different levels of diversity observed in this study. In addition to the aforementioned **R** packages, we used *TreeSim* [329] to create our theoretical communities. We created a custom function that would create two communities of equal richness with different extinction regimes and return a single dataframe with the community MPD and MNTD recorded. For both communities, we defined three time periods, each with $\lambda = 1.75$ and $\mu = 0.1$. We defined survival probability (x) manually for unstable (*i.e.*, lacking refugia) communities, and defined survival rates for stable (*i.e.*, possessing refugia) communities manually or according to Equation 1 to create a semblance of proportionality.

$$x.stable = 0.9 - x.unstable * 0.10 \tag{3.1}$$

We performed multiple iterations of these tests, and varied them from having highly disparate levels of survival (*e.g.*, 0.2 for unstable environments and 0.92 for stable environments) to similar rates of moderate survival (0.7 & 0.75) and similar rates of low survival (0.3 & 0.35). We ran 200 simulations for each scenario to get a sample distribution for comparisons between extinction rates. Distributions of MPD and MNTD were then compared with t-tests using the **R** function ‘t.test’ [286] and inspected visually using histograms.

3.4 Results

3.4.1 Richness

Our datasets included 1305 species of mammal and 2251 species of bird. We found that species richness of birds and mammals are positively correlated spatially ($P < 0.05$, adj. $R^2 = 0.85$, correlation = 0.92; $D = 0.85$, $P < 0.05$; Figure 3.1). Richness for both groups was highest in the topographically complex regions of Eastern Africa, especially in the Lacustrine Rift and the highlands from Ethiopia south to Eswatini, Lesotho, and South Africa (Figure 3.2. Both groups also show signatures of high richness across the northern edge of the Congo Basin into Cameroon. These patterns are more easily observed in birds, almost certainly because of their higher species richness on the continent. A cluster of outlier points ($n = 202$, 0.0008% of total) was identified with high mammalian species richness and low avian species richness (*i.e.*, more than 60 mammal taxa and fewer than 125 bird taxa); these areas are almost entirely from the fringes of large African lakes, where apparent spatial inconsistencies between the two databases exist.

3.4.2 Mean phylogenetic distance (MPD)

Mean phylogenetic distance differed in spatial patterning between the taxonomic groups, and, while a positive relationship between bird and mammal MPD exists, the correlation is relatively weak ($P < 0.05$, adj. $R^2 = 0.13$, correlation = 0.35; $D = 0.91$, $P < 0.05$). Birds exhibited a clear pattern of lower MPD in harsh environments (*e.g.*, the Sahara) and higher MPD in species-rich and mesic habitats (*e.g.*, the Sahel), where communities are more diverse and more basal species (*i.e.*, *Struthio camelus*) reside (Figure 4.3A). Mammals had less clearly defined zones of low MPD, with parts of the Sahara, the African Rift, and transitions between the Sahel and the humid equatorial forests possessing relatively low MPD. Higher mammal MPD values predominated in the Sahel, the Congo, and more mesic habitats of southern Africa (Figure 3.3).

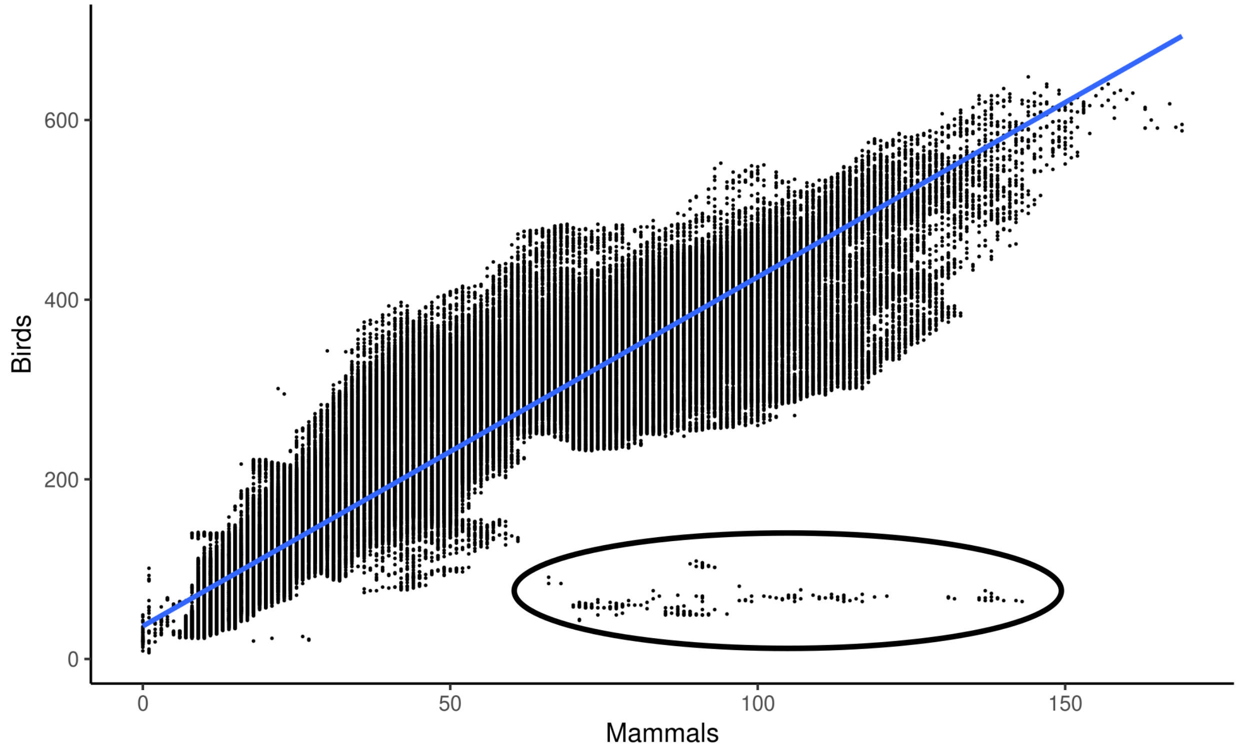

Figure 3.1: Linear regression between bird and mammal species richness across Africa. Note that the outliers (circled) denote areas close to lakes, where apparent spatial errors in mapping exist. The relationship between these mammals (m) and birds (b) can be approximated by the following equation (with 95% confidence intervals noted, and all variables supported by $P < 0.05$ and adjusted $R^2 = 0.85$): $m = 3.89b + 36.58$.

3.4.3 Mean nearest taxon distance (MNTD)

Mean nearest taxon distance was found to be more correlated between birds and mammals than mean phylogenetic distance ($P < 0.05$, adj. $R^2 = 0.48$, correlation = 0.69; $D = 0.90$, $P < 0.05$). Both groups showed lower MNTD values in the Sahara and Namib deserts, and both groups also showed a signal of relatively lower MNTD in wet equatorial forests, specifically the Upper Guinea Forests, Lower Guinea Forests, Congo Rainforest, and Malagasy Rainforests. Relatively lower values also were shared in some highland regions, *e.g.* in the Ethiopian Highlands and the Great Escarpment of Southern Africa.

3.4.4 Phylogenetic dispersion

Direct comparisons of dispersion between birds and mammals found a weak but positive correlation between these two groups ($P < 0.05$, adj. $R^2 = 0.09$, correlation = 0.31; $D = 0.94$, $P < 0.05$). After transforming data into categorical categories of dispersion, patterns were found to be significantly more similar than random ($\chi^2 = 23717$, $df = 4$, $P < 0.05$). Specifically, both groups share underdispersion in xeric habitats (most notably, the Sahara) and in many wet equatorial habitats (specifically, Africa's large tropical rainforests). Other regions with shared underdispersion include the higher elevations of Ethiopia, interior Southern Africa, and the East African Rift. Some areas of discordance in pattern between these groups include the Malagasy Rainforests (underdispersed in mammals, overdispersed in birds) and Atlas Mountains (overdispersed in mammals, underdispersed in birds).

When distilling patterns down to the level of ecoregion, we found clear associations between underdispersed communities and the Central African rainforests, the highlands of Eastern Africa, and parts of the Sahara and Maghreb. Some of the most notable regional differences between the two groups are lower phylogenetic dispersion in Madagascar for mammals (especially in the humid eastern part of the island) and lower phylogenetic dispersion for birds in Ethiopia and more broadly within the Southern African highlands (Figure 4.3).

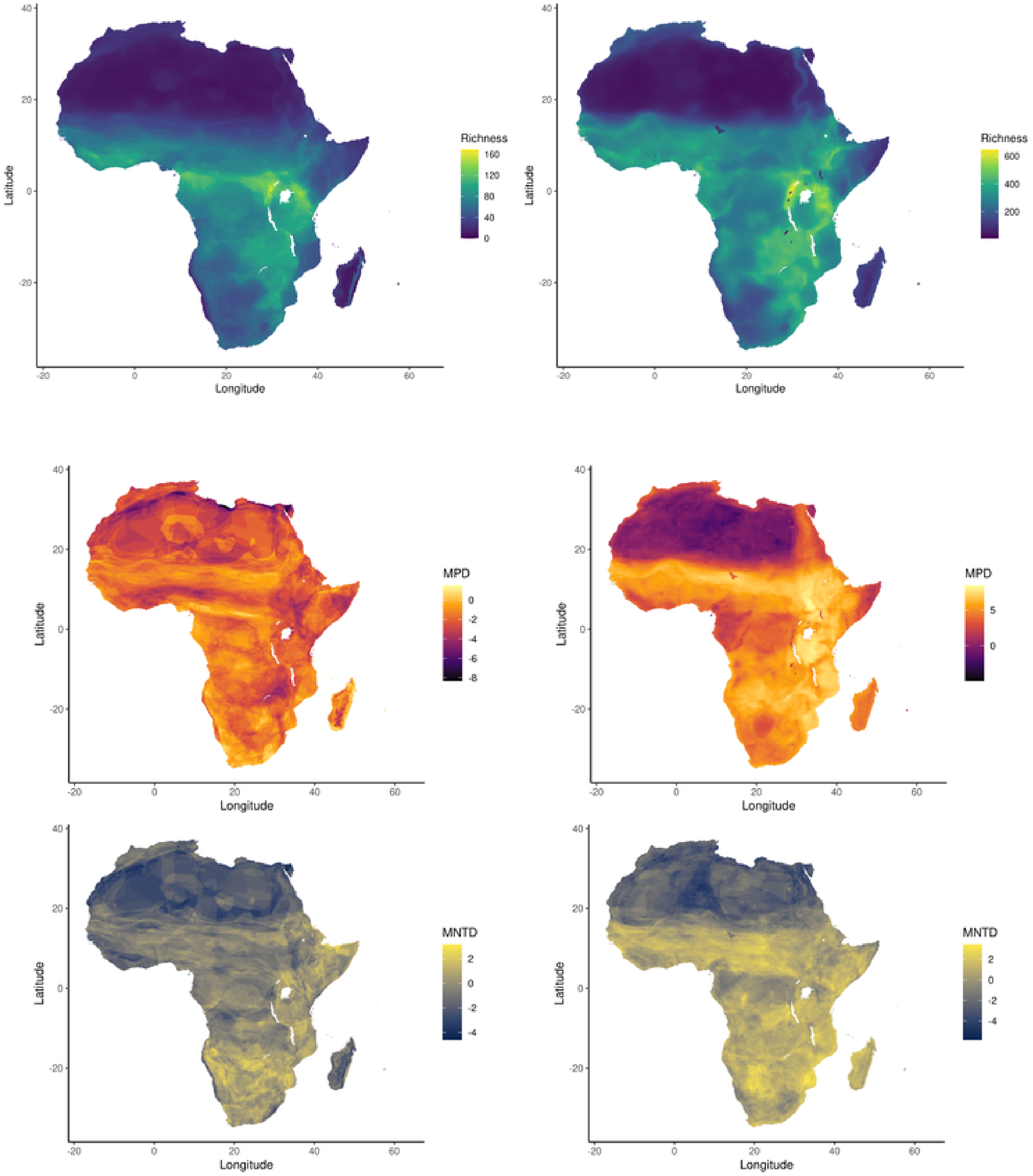

Figure 3.2: Column 1 represents metrics for mammals and column 2 for birds. 2a-2b: Cumulative species richness (alpha diversity) in Africa. 2c-2d: Mean Phylogenetic Distance (MPD) in Africa. 2e-2f: Mean Nearest Taxon Distance (MNTD) in Africa.

3.4.5 Theoretical communities

We found that, in every test performed, the average MPD and MNTD for 'unstable' communities (*i.e.*, those with higher extinction rates) exceeded those for 'stable' communities (*i.e.*, with lower extinction rates). These values were consistent, despite (sometimes broad) overlaps in the distribution of data derived from each scenario. We only observed an inability to separate these values when species diversity was low (*i.e.*, 10). Increasing the difference in extinction rates between the two communities and inflating the number of species present in a community exaggerated the disparity between MPD and MNTD distributions between the two communities.

3.5 Discussion

African mammals and birds have important differences in their evolutionary histories, but they show strong geographic correlations across Africa with respect to their community assembly, with regions associated with climatic 'refugia' possessing underdispersed communities and less climatically stable regions being more overdispersed. These areas include many regions often touted as refugia in sub-Saharan Africa, such as the equatorial rainforests and mountains in the east, as well as the Maghreb, an area that functioned as a refugia for palearctic taxa [148, 150]. Our theoretical models confirm that reduced extinction is sufficient for creating underdispersion in communities.

Previous studies on Afrotropical rainforest biodiversity have refuted the idea of evolutionary museums, pointing out large amounts of genetic diversity accumulated within continent-spanning forest taxa [171, 233]. These patterns of diversification, however, inherently point to the existence of multiple lowland rainforest refugia within the continent during past glacial cycles [352]. There is no doubt that these cycles have built diversity within this region, as evidenced by locally endemic species, but large portions of lowland rainforest assemblies are part of the same large radiations within similar habitats (e.g., Pycnonotidae throughout we

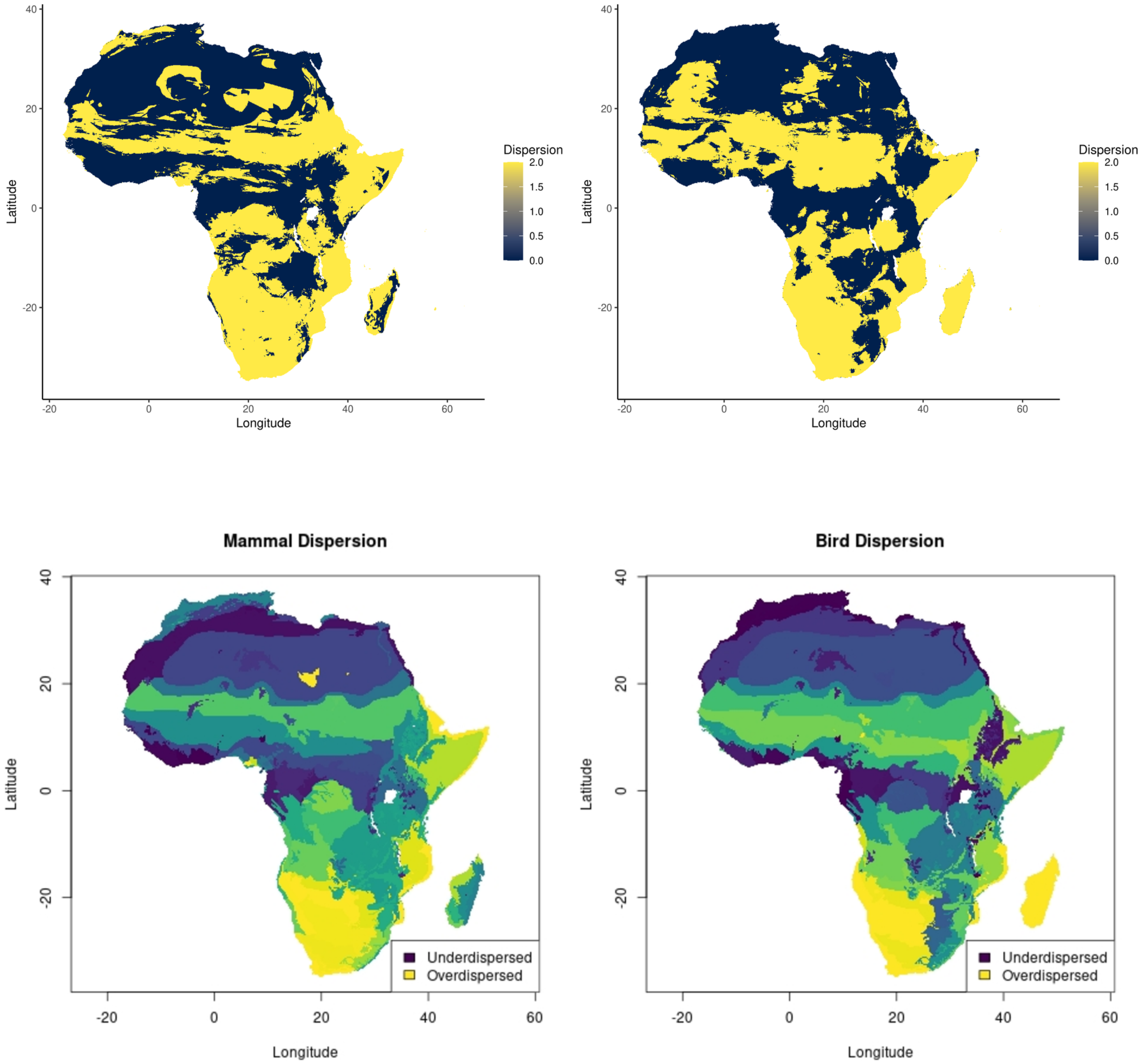

Figure 3.3: Dispersion in mammals and birds shown for individual grid cells (3a-3b, ranging from underdispersed [0] to overdispersed [1]) and for values averaged within ecoregions (3c-3d). Regional patterns that appear in the individual grid cells are accentuated within ecoregions, most notably the consistent phylogenetic underdispersion in equatorial rainforests, the Maghreb, and within the highlands of Eastern Africa. Note that some regional patterns differ between the two groups, especially within Madagascar, but the continental trends are extremely similar.

equatorial African forests) [310]. Montane areas—considered 'cradles' of evolution due to their allopatric habitats and refugia during climate cycles [113]—possess these same dynamics, and research elsewhere has shown spatial coincidence between regions that would qualify as both 'cradles' and 'museums' [12]. Our findings further this idea that refugia create museums in the sense that lineages persist and relative MPD and MNTD are decreased, but that this effect does not negate these region's ability to accumulate diversity.

Our results are conditional on the accuracy of the spatial and taxonomic data for both groups. Many Afromontane and Afrotropical lowland taxa demonstrate surprising phylogeographic patterns upon close examination, yet many multi-species studies do not incorporate all described populations to determine if existing taxonomic assessments are correct [72, 349, 352, 353]. Taxonomic conservatism, a phenomenon that predominates in birds more so than mammals, is also potentially introducing bias within these studies [359]. More thorough reviews of phylogeography and species limits are necessary to fully understand continental dynamics of diversification, although these taxonomic revisions may merely clarify which regions are 'contact zones' between refugia rather than change the patterns observed within individual communities [81]. There are documented issues with IUCN range maps (such as those used here) [156], particularly in tropical regions [108]. We find many areas with high mammal richness and low bird richness derived from these maps are along the shorelines of lakes, suggesting spatial inconsistencies in how range maps are constructed for the two groups. The detail of the taxonomic and spatial sampling of this study likely minimizes potential effects in estimated community structure regarding the inaccuracy of range margins.

Low MPD and MNTD are often inferred to be the result of environmental filtering, with the Andes being upheld as a particular example of 'niche expansion' and diversification within the limited lineages that colonized the region [137]. However, other factors (such as competition) also have been put forward as alternative causes to the same patterns as filtering [55]. At the level of Mammalia and Aves in Africa, we demonstrate that reduced rates of extinction can also lead to these similar patterns. Thus, patterns of filtering (*i.e.*, underdispersion) can be obfuscated by environments that coincide with biogeographic refugia. It is therefore important to consider the biogeographic history of the clade and species being studied when determining the cause of underdispersion patterns. Underdispersion within specific environments across multiple families and classes of organisms is linked to climatic stability and the persistence of lineages that have diversified in situ within the greater metacommunity during disjunctions in spatially discrete refugia. Environmental filtering may be a cause of reduced MPD and MNTD for certain regions and certain lineages (such as within Afromontane *Cinnyris*) [45], but our findings indicate environmental filtering may also be an illusion of specific environments having reduced extinction while maintaining high levels of diversification. Thus, despite Afromontane regions being considered hotspots for diversification [112, 113, 287], similar patterns of diversification will also occur in other geographic regions when environmental cycling creates similar patterns of habitat fracturing with stable refugia, as demonstrated by the Afrotropical rainforests [170, 171, 233, 354] and the Maghreb [148].

Regional differences in phylogenetic dispersion illuminate how climatic cycles have shaped the bird and mammal diversity of the African continent. The disparities observed between mammals and birds highlight the differential short-term responses of these communities to climate change while also highlighting how shared refugia result in similar patterns for both groups through evolutionary time [297]. Both birds and mammals show high richness, high MPD, and high MNTD in Eastern and Southern Africa. These areas are home to some of the most topographically complex regions within Africa, including the highest (Kilimanjaro, 5895 m asl) and lowest (Lac Assal, -155 m asl) elevations on the entirety of the African continent. In addition to hosting large amounts of habitat variability, the African Rift region is relatively centrally located within the continent (and thus relatively central for species' dispersing across the continent) (Cooper, in review). This variety has resulted in the persistence of some phylogenetic outliers (e.g., *Xenoperdix*) [90, 113], but the overall pattern of underdispersion is still maintained. Notably, while locally endemic species are often associated with montane habitats, humid and montane microhabitats in the otherwise xeric regions of Africa are also home to restricted range species and taxonomic outliers, such as Togo Mouse *Leimacomys buettneri* and Ethiopian Bushcrow *Zavattariornis stresemanni* [91, 199].

Madagascar shows some of the clearest disparities between mammals and birds within our study, perhaps due to the nature of colonization frequency and pattern by birds and mammals [104, 291] coincident with the museum-like nature of islands for taxonomic groups that are no longer found in continental settings [201, 238]. Notably, the insular nature of Madagascar makes it theoretically more accessible to birds than to terrestrial mammals. Indeed, for birds, we see island wide overdispersion, undoubtedly related to the co-occurrence of 'recent' colonists with more 'ancient' lineages found throughout the island (e.g., Brachypteraciidae, Mesitornithidae, etc.). Mammals, however, are dominated by older groups with modern current patterns in the ocean working against novel colonization. In this group, where lineages have been isolated on the island for a greater amount of time, we see a repeat of the same patterns as mainland Africa. Wetter eastern rainforests, areas that have been identified as climatic refugia [288, 290], possess underdispersed communities relative to the xeric western regions.

Phylogenetic patterns were more highly structured for birds than for mammals. This is driven in part by distributions and taxonomy for birds being more well known, with many African mammal complexes (specifically shrews, rodents, and bats) still possessing large amounts of taxonomic flux [175, 244, 250]. It is also possibly attributable to differential responses to climate change between the two groups on shorter timescales [297]. Nevertheless, we recovered positive correlations between the MPD and MNTD of both groups, and the spatial distribution of over- and underdispersed regions overlap extensively. Overdispersed communities for both groups are concentrated in xeric and semi-arid habitats across the continent (with the notable exception of the Sahara), with underdispersed communities being concentrated in low elevation rain forest and high elevation habitats across the continent.

3.6 Conclusions

Underdispersion has often been associated with environmental filtering or with limited dispersal within or between specific environments. An overlooked consideration is that stability, in the form of refugia, and depressed extinction rates may result in these same patterns, and that both montane and lowland regions can exhibit similar patterns when both possess similar patterns of stability. In Africa, underdispersion in mammals and birds is clearly linked to climatic refugia, suggesting that underdispersion at large taxonomic scales can be caused by relative extinction rates.

3.7 Acknowledgments

Foremostly, I am thankful to my co-authors, Nicholas M.A. Crouch, Adam Ferguson, and John M. Bates. We thank the many researchers, scientists, and community members who have influenced the way we think about the diversity and evolution of birds and mammals not just in Africa, but worldwide. Specifically, we would like to single out the Hackett-Bates Lab and the Cooper-Garrod discussion group. We also thank J. M. G. Caparucho, C. Cooper, and S. J. Hackett. We thank the Committee on Evolutionary Biology and the Department of Geophysical Sciences, University of Chicago for access to their clusters for analyses.

3.8 Ethics statement

This study is based entirely upon data and code that are available free for use, and data and codes used herein are likewise available for further use.

3.9 Data availability

Codes used in this study are available in Appendix and on Dryad [82].

CHAPTER 4

HIERARCHICAL ANALYSES OF AVIAN COMMUNITY BIOGEOGRAPHY IN THE AFROMONTANE HIGHLANDS

4.1 Abstract

The Afromontane mountains are a complex series of highlands that have intermittently been connected by habitat corridors during climatic cycles, resulting in a mosaic of range disjunctions and allospecies complexes in the present day. Patterns of community relatedness between geographic regions are often determined through single-species analyses or spatial analyses of diversity and nestedness at the species level. To understand patterns of Afromontane community evolution and to assess the effects of taxonomy on our understanding of biogeographic patterns, I concatenated three different lists of Afromontane bird taxa divided into five different taxonomic hierarchies. These lists were converted into a presence-absence matrix across 55 different montane regions, and analyzed using multiple different clustering techniques using a replicable coding pipeline. I use these lists and methods to determine patterns of relatedness between montane blocks, to assess the consistency with which biogeographic regions are recovered, and to shed more light on patterns of connectivity within the Afromontane region. Results reaffirm the distinctiveness of many different biogeographic regions (i.e., the Cameroon Highlands) while also clarifying regional relationships and the presence of 'transition zones' between regions. Differences between lists illustrate how our understanding of taxonomy and distribution in the Afromontane highlands can also change our understanding of Afromontane biogeography. Most notably, I find evidence for an Expanded Eastern Arc that includes the Eastern Arc Mountains and highlands in Malawi, Mozambique, and Zimbabwe. This study presents a rigorous yet easily adjustable pipeline for studying regional biogeography from multiple perspectives with classical and novel approaches.

4.2 Introduction

For hundreds of years, scientists have studied the ways in which montane communities are assembled and maintained [287]. Within Africa, complex patterns of regional endemism and large range disjunctions within single species or between related taxa complicate our understanding of connectivity between extant montane habitats [45, 93, 152, 215]. Many of these patterns of disjunction and local endemism appear to result from two complementary processes: environmental changes that have allowed for ranges to expand and contract through time (*i.e.*, the Turnover-Pulse Hypothesis) and relatively stable climates in montane regions that allow for diversification and while buffering against extinction [112, 113, 275, 355]. An example of both phenomena is the phasianid genus *Xenoperdix* Svendsen *et al.* 1994, a relative of Southeast Asian *Arborophila* Hodgson 1837. This relict genus has been able to persist in the Eastern Arc highlands of Tanzania, where the complex regional geography and climatic cycling has promoted the differentiation of two geographically proximate (but allopatric) populations that are often regarded as separate species [46, 90].

The distributions of African taxa lend credence to the hypothesis that climatic cycling has resulted in modern distributions of flora and fauna, by way of 'corridors' of suitable climatic conditions that linked disparate montane blocks [45, 72, 93, 113, 198, 275, 355, 368]. The relative likelihood of vicariance vs. dispersal (or range expansion) during these climatic cycles varies with respect to species' life history, morphology, and migratory habits [29, 79]. Within the Afromontane avifauna, different magnitudes of separation exist, with some taxa belonging to well-differentiated superspecies spread across the continent (*e.g.*, the arboreal *Turdoides* Cretzschmar 1926 [*Kupeornis* Serle 1949]) while others show no obvious differentiation across widely separated populations (*e.g.*, *Ploceus insignis* [Sharpe 1891]) [31]. The consistency of overlap between these regions with respect to the distributions of species of varying levels of diversification suggest that similar colonization patterns led to modern distributions for a majority of taxa.

These resulting broad-scale patterns of distributional overlap of avian montane lineages in Africa have been used to develop hypotheses of biogeographic relationships for multiple taxonomic groups [93, 138, 152, 198, 215]. Previous studies of relationships have been based on hierarchical clustering (*e.g.*, UPGMA 'bottom-up' clustering) [138, 215], nestedness [75], and other methods of comparing composition, including Simpson's index [316] to account for the low richness inherent to satellite montane blocks [93]. These studies rely both on the widespread nature of individual taxa (*e.g.*, *Ploceus insignis* [Sharpe, 1891]) and on the distribution of 'superspecies' that consist of multiple allopatric taxa that are or appear to be closely related [93, 152]. These studies have reinforced the distinctiveness of many Afromontane blocks, such as the Ethiopian Highlands, while reinforcing the apparent connections of others, such as the ties between the avifaunas of the Cameroon Line and the Lacustrine Rift (also known as the Albertine Rift). Many of these studies have also sought to determine the number of biogeographic regions that exist within the African continent; the methods for this determination vary, but often rely heavily on the author's interpretation of their clustering method and knowledge of the flora and fauna. Past biogeographic assessments are further complicated by shifting taxonomy, as new Afromontane bird species are still being described *de novo* [46, 353] and existing taxonomic treatises are changing with additional genetic, morphological, and ecological information [46, 48, 49, 72, 260].

In order to address overall patterns of Afromontane biogeography in concert with changing taxonomy, I adapted a table of montane bird taxa from previous authors into a presence-absence matrix for 55 different montane regions (Figure 4.1; Table B.1). This matrix is divided hierarchically into different taxonomic schemes to best reflect our understanding of Afromontane diversification at different taxonomic levels (and, theoretically, with varying amounts of time [accumulated diversification] being used to define taxa). I analyze these data with multiple different clustering methods to determine 1) the relationships between different montane regions, 2) the robustness of these relationships between authors and methods, and 3) to identify which regions are 'core' montane regions and which regions are 'transitional' between montane regions. Furthermore, I present this analysis pipeline in its entirety

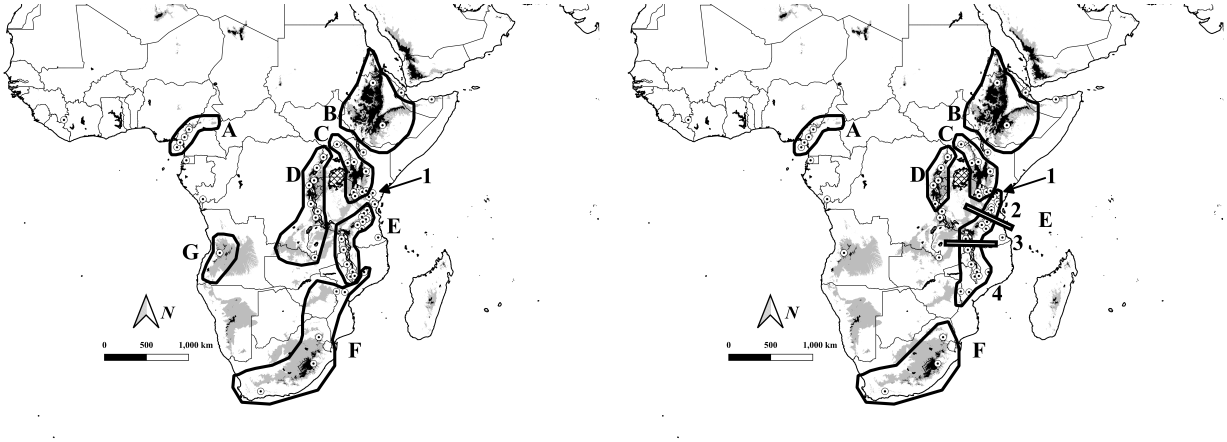

Figure 4.1: A map of sub-Saharan Africa with study localities shown as white dots with black centers. Elevations of <1250 m are shown in white, elevations 1250-1750 m are shown in gray, and elevations of >1750 m are shown in black. Country boundaries (thin black lines) are superimposed and lakes are shown with cross-hatching. Approximated biogeographic regions defined by Dowsett (1986; left) and from the 2021 list in this study (right). Lettering refers to the following areas, with names corresponding to Dowsett (1986)/2021 list: A) Cameroon/Cameroon Highlands; B) Ethiopia/Ethiopian Highlands; C) Kenya/Kenya-Tanzania; D) East Congo/Lacustrine Rift; E) Tanganyika-Nyasa/Expanded Eastern Arc; F) Southeastern/Southern Great Escarpment; and G) Angola (region not in 2021 list). For the 2021 list at right, subregions of the Expanded Eastern Arc are as follows, with approximate borders shown as bars across the biogeographic region: 1) Taita Hills; 2) Northern Eastern Arc (Pare Mountains to Malundwe/Rubeho); 3) Central Eastern Arc (Uluguru to Nyika); 4) Southern Eastern Arc (alternatively, Malawi-Mozambique; Dedsa-Salima to Chimanimani Mountains). Note the seventh region for the 2021 list (satellite regions) corresponds to all points not encapsulated in a biogeographic envelope. Figure created in QGIS 3.18.2 [281] with elevation data from [4].

such that these analyses can be repeated in the future as our knowledge of the Afromontane avifauna improves.

4.3 Methods

All analyses were performed in **R** 4.0.3 [286] with general data organization relying on the **R** packages *data.table* [92], *maps* [24], *rnaturalearth* [328], *tidyverse* [370], and *viridis* [125]. I also referenced ColorBrewer 2.0 (`https://colorbrewer2.org`) for assistance with plots.

4.3.1 Species dataset

I adapted a matrix of montane bird taxa from Dowsett [93] and Bowie [45] to a more recent taxonomy [63] and created a presence absence matrix of Afromontane birds for 55 sub-Saharan Afromontane sites (Table B.1). These localities are generally well-known larger montane regions that are distributed throughout Sub-Saharan Africa, with some less species-rich 'satellite ranges' included as well. I expanded this list from the aforementioned authors by including taxa with endemic montane populations that are more widespread outside of the study region (*e.g.*, *Anthus similis* [Jerdon 1840]), taxa that are found in lower-lying montane regions that are more xeric (*e.g.*, *Linaria johannis* in the Somalian Highlands), taxa that are geographically restricted around highland regions (*e.g.*, *Monticola rupestris* [Vieillot 1818]), and taxa that are elevational migrants within specific montane regions (*e.g.*, *Vanellus melanopterus* [Cretzschmar 1829]) (hereafter, the '2021 list'; Table B.2). Thus, the taxa I added to the montane species list are affiliated with montane regions (as determined by habitat and distribution), but they are not restricted to a specific elevation or habitat type like Dowsett [93] or Bowie [45]. I referenced published habitat information and subspecific distributions from aggregated sources to create the presence absence matrix [31, 43, 63, 317]. Taxa not within the study area's montane regions (*e.g.*, *Sylvia lugens clara* [Meise 1933]), taxa that migrate between highland regions latitudinally (*e.g.*, *Sarothrura ayresi* [Gurney 1877]), and taxa that are locally montane but occur broadly in lower elevations within the tropical latitudes (*e.g.*, *Tauraco livingstonii* [Gray, 1864]) were excluded from all iterations of the analyses (Table B.3).

I analyze species distributions at five different taxonomic hierarchies: Genus, Superspecies, Species, Group, and Subspecies. Taxonomic hierarchies and taxonomy implemented can affect the patterns recovered by scientists, and understanding the bias introduced by human classification is an important facet of biogeographical studies [111]. Genus, Species, Group, and Subspecies are derived from the eBird/Clements checklist [63], wherein 'groups' are used within the eBird taxonomy for related and/or similar and presumably related taxa.

For example, *Campethera tullbergi* (Sjöstedt, 1892) possesses two phenotypically differentiable Groups, *tullbergi* and *taniolaema/hausburgi*, which have been considered as a monotypic *C. tullbergi* and polytypic *C. taniolaema* by some authors [129]. Superspecies are derived from historical taxonomies and from known and/or presumed relationships between taxa [31]. This category is an attempt to replicate the superspecific category used by Hall and Moreau [152] and others to elucidate biogeographic patterns. This assignation has evolved with published genetic data highlighting allospecies relationships between populations formerly considered conspecific (*e.g.*, the *Laniarius fuelleborni* complex [Reichenow 1900]) [353]. Many presumed superspecies are not grouped together due to ambiguities regarding their relationships (*e.g.*, arboreal *Turdoides* [*Kupeornis*] are sometimes considered a single superspecies, but are considered separately herein) [93, 152].

4.3.2 Geographic similarity

Jaccard indices of similarity (S) a calculated for the 2021 list using the function 'vegdist' in the package *vegan* [252]. This index provides a value from 0 (identical communities) to 1 (completely different communities) for comparing community composition between sites. An accompanying matrix of geographic distances between localities was drawn from approximate midpoints of mountains and the coordinates of the highest peaks of mountains (`https://google.com/maps`; `https://www.wikipedia.org`; Table 4.1), with distances between these localities being calculated with the function 'dist.m' in *geosphere* [159]. I performed mantel tests to compare the similarity and distance matrices using 'mantel' with the method of 'spearman' in *vegan* [252].

Table 4.1: Montane regions used in this study, ordered approximately from Northwest to Southeast. Each region is listed with its name, region (according to the 2021 list's hierarchical clustering; Figure 4.4), coordinates, and additional notes. In general, elevations conform to the highest point within a given highland in meters asl, and coordinates refer to either the highest point or an approximate midpoint.

#	**Locality**	**Region (2021)**	**Long.**	**Lat.**	**Elev.**	**Note**
1	Upper Guinea Highlands	Satellite Regions	−8.42	7.64	1752	
2	Bioko	Cameroon Highlands	8.70	3.50	3012	
3	Mt. Cameroon	Cameroon Highlands	9.17	4.22	4040	
4	Cameroon Highlands	Cameroon Highlands	9.83	5.03	2411	
5	Bamenda & Adamawa	Cameroon Highlands	10.52	6.20	3011	
6	Monte Alen	Satellite Regions	10.11	1.53	1200	
7	Lendu	Lacustrine Rift	30.86	2.01	2455	
8	West Rift	Lacustrine Rift	28.69	−2.25	3475	Mt Kahuzi coordinates; includes Itombwe; high elev for Itombwe given
9	Rwenzori	Lacustrine Rift	29.87	0.39	5109	
10	East Rift	Lacustrine Rift	29.45	−1.51	4507	Mt Karisimba; includes Kibira-Nyungwe

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Table 4.1, continued.

#	Locality	Region (2021)	Long.	Lat.	Elev.	Note
11	Kabobo	Lacustrine Rift	28.97	−5.06	2700	
12	Marungu	Satellite Regions	29.69	−7.13	2460	
13	Mahale	Satellite Regions	30.00	−6.20	2462	
14	Somalia	Satellite Regions	47.25	10.74	2460	Shimbiris
15	Djibouti	Satellite Regions	42.66	11.75	1650	Day Forest
16	West Ethiopia	Ethiopian Highlands	38.37	13.24	4550	
17	East Ethiopia	Ethiopian Highlands	39.82	6.83	4377	
18	S Eth-NKen	Satellite Regions	36.92	2.73	2285	Kulal as reference
19	Imatong	Kenya-Tanzania	32.91	3.95	3187	
20	Elgon	Kenya-Tanzania	34.53	1.12	4321	
21	West Kenya	Kenya-Tanzania	35.50	1.27	3530	Cherangani Hills
22	Kenya-Aberdare	Kenya-Tanzania	37.31	−0.15	5199	
23	Ngorongoro	Kenya-Tanzania	35.44	−3.28	3206	Oldeani
24	Mbulu	Kenya-Tanzania	35.66	−3.88	3420	Hanang for elevation
25	Meru	Kenya-Tanzania	36.75	−3.25	4562	
26	Kilimanjaro	Kenya-Tanzania	37.35	−3.08	5895	

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Table 4.1, continued.

#	Locality	Region (2021)	Long.	Lat.	Elev.	Note
27	Taita	Expanded Eastern Arc	38.33	−3.42	2228	
28	Pare	Expanded Eastern Arc	37.75	−4.00	2463	
29	W Usumbara	Expanded Eastern Arc	38.39	−4.75	2220	Estimated from Google
30	E Usumbara	Expanded Eastern Arc	38.65	−5.11	1240	Estimated from Google
31	Nguu	Expanded Eastern Arc	37.47	−5.55	1550	
32	Nguru	Expanded Eastern Arc	37.50	−6.00	2400	
33	Ukaguru	Expanded Eastern Arc	37.00	−6.47	2250	
34	Rubeho	Expanded Eastern Arc	36.70	−7.02	2286	
35	Uluguru	Expanded Eastern Arc	37.67	−7.17	2630	
36	Malundwe	Expanded Eastern Arc	37.30	−7.40	1290	
37	Udzungwa	Expanded Eastern Arc	36.82	−7.77	2579	
38	Mahenge	Expanded Eastern Arc	36.67	−8.82	1440	Estimated from Google
39	Iringa	Expanded Eastern Arc	36.03	−8.24	1800	Estimated from Google; Iringa sector of Udzungwas
40	Nyika	Expanded Eastern Arc	33.60	−10.35	2605	
41	Kaningina	Expanded Eastern Arc	33.92	−11.99	1860	Estimated from Google

Continued on following page.

Table 4.1, continued.

#	Locality	Region (2021)	Long.	Lat.	Elev.	Note
42	Dedsa-Salima	Expanded Eastern Arc	34.43	−14.20	2000	Estimated from Google
43	Zomba	Expanded Eastern Arc	35.29	−15.33	2087	
44	Thyolo	Expanded Eastern Arc	34.95	−16.05	1400	Estimated from Google; Michiru Mts Cons Area
45	Mulanje	Expanded Eastern Arc	35.59	−15.95	3002	
46	Namuli	Expanded Eastern Arc	37.03	−15.37	2419	
47	Gorongosa	Expanded Eastern Arc	34.11	−18.40	1863	
48	Chimanimani	Expanded Eastern Arc	32.84	−18.30	2592	Includes all East Highlands
49	N ZA	S Great Escarpment	30.17	−25.21	2274	Steenkampsberg given for general highland area; Northern Drakensberg
50	Drakensberg	S Great Escarpment	29.36	−29.20	3450	Mafadi
51	Cape Highlands	S Great Escarpment	21.37	−33.40	2325	
52	Zambia	Satellite Regions	29.57	−13.17	1400	General elevation given; large elevated area and not a specific range

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Table 4.1, continued.

#	**Locality**	**Region (2021)**	**Long.**	**Lat.**	**Elev.**	**Note**
53	Angola	Satellite Regions	15.17	−12.47	2620	
54	Rondo Plateau	Satellite Regions	39.16	−10.14	920	Estimated from Google
55	Mayombe	Satellite Regions	12.62	−4.34	930	Mt Foungouti

4.3.3 Clustering methods

Overall similarity between montane regions and the ideal number of clusters for said regions was determined using k-means clustering. This method (function 'kmeans' in **R**) divides data points into a set of k groups around k centers such that the sum of squares in each group is minimized [286]. The performance of different levels of k was assessed using gap-statistic analyses using the function 'fviz_nbclust' in the **R** package *factoextra* [194]. For the best k, group assignments for highland regions were saved for each dataset and for each taxonomic level.

Geographic patterns were assessed using hierarchical clustering via the unweighted pair group method with arithmetic mean (UPGMA) using the base **R** command 'hclust' [286]. This is a 'bottom up' method that groups the most similar regions at each step, thereby determining similarity in a stepwise fashion that can be easily viewed (and divided into groups) using dendrograms [286]. This method can result in different groupings than k-means clustering, but can be more difficult for determining the number of clusters. Thus, I use the number of clusters determined from k-means to provide a non-biased assessment for the number of clusters for the dendrograms. However, I also assess clear breaks in the dendrograms qualitatively to estimate the number of biogeographic clusters, most notably for consensus dendrograms created from all taxonomic hierarchies for a particular list.

Lastly, I visualize the inherent geographic structure of populations using the **R** package *ecostructure* [366, 367]. This program emulates the genetic algorithm STRUCTURE [168] to parse presence-absence matrices into different geographic motifs. Similar to k-means clustering, this method can be applied across a spectrum of group sizes (K) to study the geographic structuring of communities. Unlike other methods employed herein, ecostructure also allows for viewing 'admixture' between community motifs, allowing for clearer interpretation of connectivity between montane regions in a format that is not limited by group assignment or dendrogram formation. I performed iterations of ecostructure for K of 2-14 for each taxonomic hierarchy in the 2021 list, with particular attention paid to the number of groups

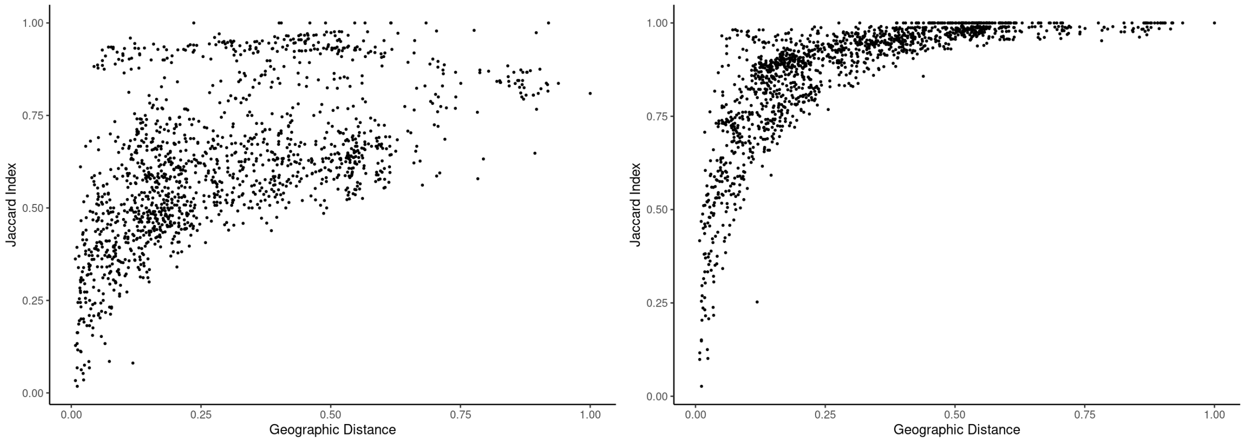

Figure 4.2: Jaccard index vs. geographic distance for the ranks of genus (left) and subspecies) right using the 2021 list. Patterns of increasing Jaccard index with increasing geographic distance are constant across all taxonomic hierarchies but the patterns and rate at which these changes occur increases with taxonomic specificity.

determined from *k*-means clustering.

4.4 Results

For all taxonomic levels, the list derived from Dowsett [93] has the fewest lineages represented, while Bowie [45] has an intermediate level of taxa and the 2021 list has the greatest number of taxa (Table 4.2). Using the number of species as an example, these lists possessed 266, 315, and 359 taxa, respectively.

Jaccard indices demonstrate a significant relationship between geographic distance and community dissimilarity for all taxonomic levels (all $P < 0.05$). Community dissimilarity increases with geographic distance, although the magnitude and rate at which community differences accumulates depends on the taxonomic scale, with finer scales (*e.g.*, subspecies) accumulated differences between communities faster than coarser scales (*e.g.*, genus; Figure 4.2). Thus, while geographic proximity correlates with community relatedness, many regions in the same geographic area can still have fairly dissimilar communities.

The optimal number of clusters for subdividing the Afromontane highlands varies by source list and by taxonomic level, with an average of 9 clusters from the Dowsett [93] list, 6.8 clusters from the Bowie [45] list, and 8.2 clusters from the list presented in this study (Table 4.2). Cluster numbers are most similar between lists for the hierarchical levels of superspecies (= 7.33, = 1.53), species (= 6.33, = 0.58), and group (= 7, = 1.73); genus (= 11, = 3.46) and subspecies (= 8.33, = 2.31) demonstrate the largest variation in cluster number between lists. The largest number of groups recovered is 15 for genus from Dowsett [93], and the smallest number of groups is 6 from multiple sources (Bowie [45]: Superspecies, Species, Group; 2021 list: Species, Group). These ideal cluster numbers from *k*-means analyses is sensitive to species inclusion, with some large changes affected by the inclusion or exclusion of wide-ranging taxa (*e.g.*, *Muscicapa adusta* [F. Boie 1828]).

Through all methods, several biogeographic regions are recovered that largely correspond to those noted in the literature. The consensus diagram for all lists contains a large polytomy (9 groups; 3-11 as enumerated here) and possesses 11 major clusters in the UPGMA tree: 1) the Ethiopian Highlands; 2) Lacustrine Rift (including the Lendu Plateau and Mt. Kabobo); 3) the Cameroon highlands; 4) the Southern Great Escarpment; 5) the Kenya-Tanzania highlands (with a northern and southern subgroup); 6) the Taita Hills; 7) the Usambara & Pare Mountains; 8) the Northern Eastern Arc (Nguu to Malundwe); 9) the Southern Eastern Arc (Uluguru & Udzungwa Mountains to Nyika); 10) Malawi-Mozambique; and 11) the satellite regions (including Angola). Consensus trees for Dowsett [93] and Bowie [45] resulted in 8 and 14 groups respectively. The 2021 list consensus has 7 major biogeographic regions: 1) the Ethiopian highlands, 2) the Lacustrine Rift; 3) the Kenya-Tanzania Highlands; and a polytomy of 4) the Southern Great Escarpment, 5) the Cameroonian Highlands, 6) an Expanded Eastern Arc (stretching from Taita in the north to Chimanimani & Gorongosa in the south with a polytomy of 4 subgroups), and 7) the satellite regions (including Angola; Figure 4.1 & 4.3). Surprisingly, the Dowsett [93] consensus list has the fewest polytomies, with the 2021 list having the only second order polytomy of the Expanded Eastern Arc being enclosed within the polytomy of the satellite regions, the Cameroon Highlands, and the Southern Great Escarpment (Figure 4.4). Major regions are largely conserved through

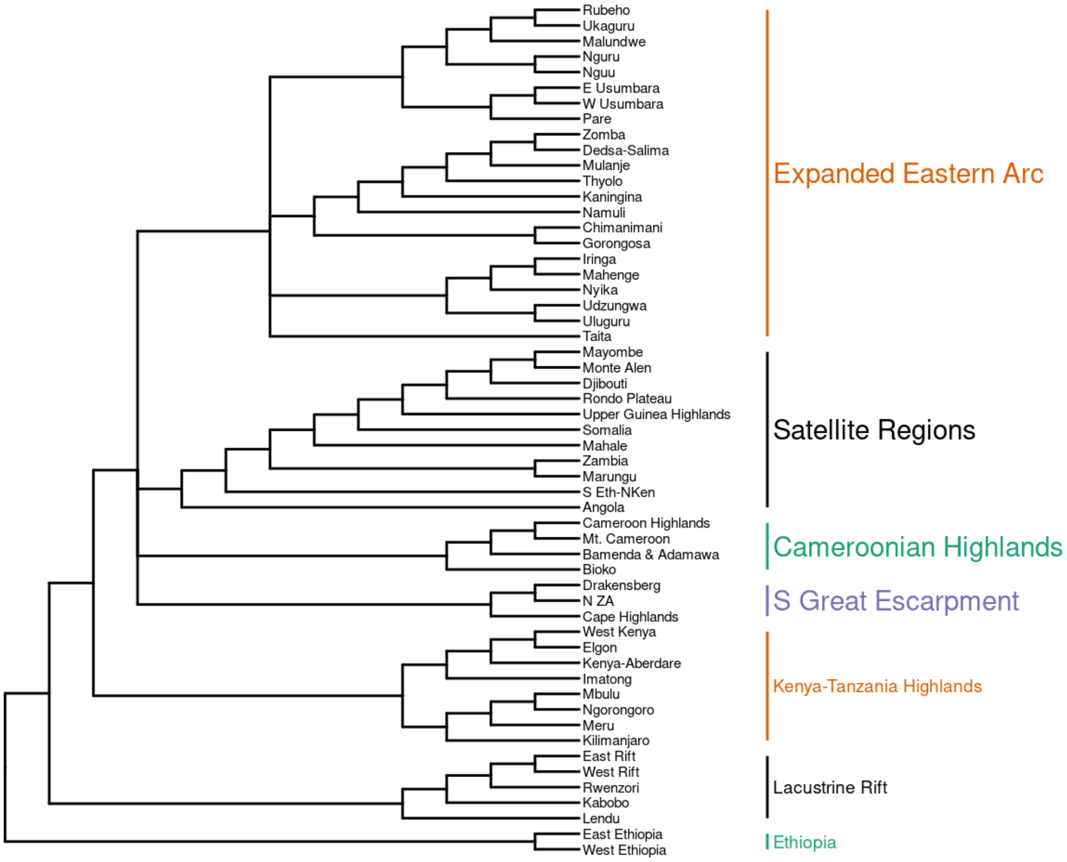

Figure 4.3: Consensus tree across all taxonomic levels for UPGMA clustering on the 2021 species list presented herein, denoting major biogeographic regions defined within the text.

all sources, though the topology of these relationships within the dendrograms varies. The Northern Tanzania and Kenya-Uganda Highlands, however, are invariably sister clusters within dendrogram analyses, hence their consideration as a single biogeographic entity (the Kenya-Tanzania Highlands) with two subregions.

Furthermore, satellite regions are frequently grouped together, and transitional ranges between biogeographic regions vary in their placement. Polytomies and the changing placement of specific montane localities within the UPGMA dendrograms reflect patterns of historical connectivity and colonization in the formation of montane communities. Transitional regions (*i.e.*, regions at the flanking edges of 'core' biogeographic regions) and regions that have been built by repeated colonization events from larger montane blocks can 'jump' between biogeographic clusters depending on the taxonomic level being used. For example, in the consensus dendrogram for the 2021 list, the Taita Hills are an independent part of a polytomy with clusters representing the rest of the Eastern Arc and highlands within Malawi, Mozambique, and Zimbabwe, reflecting both their own uniqueness and the connectivity they possess with adjacent biogeographic regions (Figure 4.4).

The addition or subtraction of species from the presence-absence matrix has less of an effect on the topology of the tips of UPGMA dendrograms and ecostructure outputs, and instead more greatly affects the ideal number of groups in *k*-means analyses and higher-order relationships within dendrograms. As mentioned, satellite regions with low species richness (low diversity) are clustered together in all methods. Widely disparate regions that share few (if any) species inherently share a lot of absences, leading to their aggregation. Higher-order differences in dendrograms are perhaps best exemplified by the differences between the consensus trees based on each list (Figure 4.4).

Similarly, the clusters derived by *k*-means revealed connectivity between transitional regions and the main biogeographic regions they connect, demonstrating some of the same patterns as the UPGMA dendrograms. Notably, this includes the occasional grouping of the Lendu Plateau with the Cameroon Line rather than the adjacent Lacustrine Rift. The hierarchical levels also revealed interesting patterns of disjunction within the modern distributions of genera and superspecies, illustrated by the fact that some iterations of the *k*-means algorithm grouped the Southern Great Escarpment with the geographically disparate Ethiopian Highlands. While clear connections between these highlands exist (*e.g.*, *Gypeatus barbatus* Linnaeus 1758 and the genus *Heteromirafra* Grant 1913), it is unclear whether these disjunctions are due to dispersal during climatic cycles, extinction of these lineages from intervening ranges, or a combination of the two. Plots derived from ecostructure more clearly illustrate these patterns of connectivity, with many intermediary regions showing admixture from multiple biogeographic motifs (Figure 4.5). Regions, such as the Taita Hills, are shown to be the result of admixture from multiple biogeographic sources rather than assigned to their own cluster or to one of their flanking clusters.

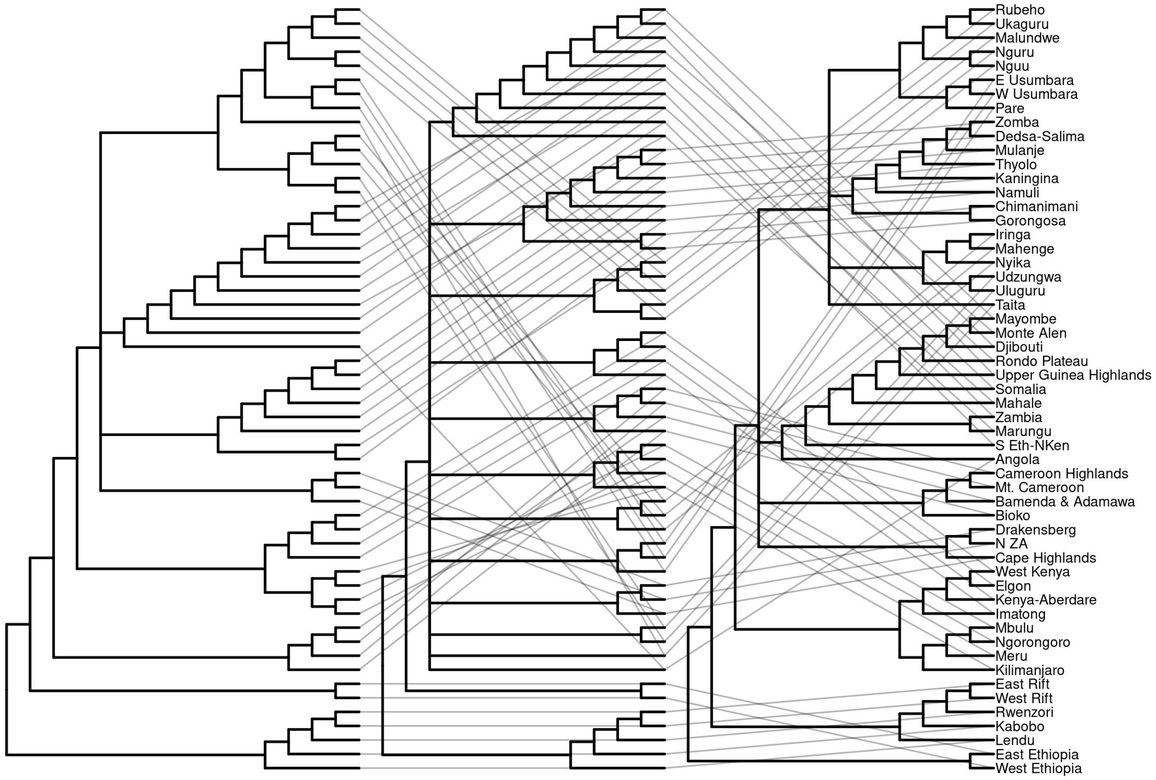

Figure 4.4: Consensus trees across all taxonomies for clustering via UPGMA performed for the species lists derived from Dowsett (1986; left), Bowie (2003, center) and the 2021 list presented herein (right). While relationships between individual montane blocks are largely maintained, the relationships between larger biogeographic areas shift between lists.

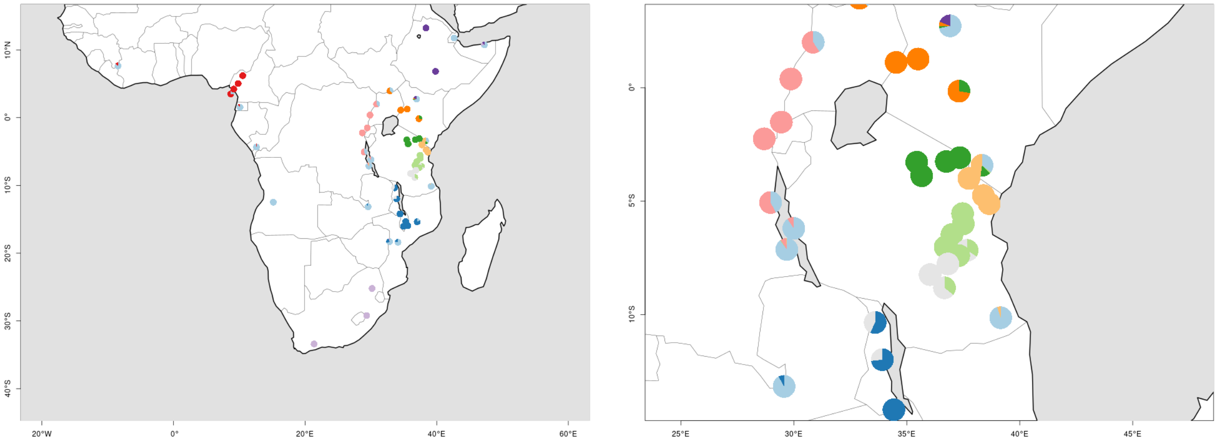

Figure 4.5: *Ecostructure* assignments for Afromontane regions using $k = 11$, the ideal number of k-means groups determined for the 2021 species list. At left, broad scale continental clusters are apparent. At right, fine-scale analyses highlight the admixture present in transitional regions between biogeographic motifs, indicated by the presence of multiple colors in a given pie chart. Inset is centered on Tanzania, showing the Lacustrine Rift (pink), Kenya-Tanzania subgroups (orange and dark green), the Northern Eastern Arc (tan), the Pare & Usambara Mountains (tan), the Northern Eastern Arc (light green), the Central Eastern Arc (silver), the Southern Eastern Arc (*a.k.a.* Malawi-Mozambique in dark blue), and satellite regions (light blue).

4.5 Discussion

This work presents a comprehensive, continent-scale analysis of Afromontane avian biogeography using multiple statistical techniques and multiple different species lists. By using these different clustering techniques, I demonstrate the ways in which highlands are connected and the ways in which complex biogeographic histories can confound straightforward interpretations of biogeographic clustering. This methodology has confirmed the stability of many local-scale patterns of biogeographic clustering with regards to regions such as the Lacustrine Rift and Southern Great Escarpment. Larger order clustering varies, however, with the regions I elucidate here differing from those outlined by Dowsett [93] and from those derived from the groupings of Bowie [45]. Previous categorization efforts relied primarily on a single method of clustering, be it on the distribution of superspecies [152], upon differing patterns of nestedness [75, 93], or on alternative clustering methods, most notably UPGMA [138, 215]. Here, I combine methods employed by previous authors with additional techniques for visualizing community composition, such as ecostructure analyses that allow novel perspectives into the motifs contributing to transitional montane block communities [366, 367].

Perhaps the most similar previous analyses to this effort for Afro-montane birds are those performed by Graham *et al.* [138] and Dowsett [93]. Graham *et al.* [138] employed extensive use of UPGMA dendrograms to understand the pattern and structure of 23 montane sites in the Cameroon Highlands. Their analysis shows varying patterns of regional grouping at different hierarchical scales, and varying patterns at different levels of species inclusion (*i.e.*, complete communities vs. only regional endemics). Specific core areas were consistently recovered as 'groups' (*e.g.*, the Adamawa Plateau), but other transitional or satellite highlands (*e.g.*, Ngel-Nyaki) were difficult to place and often grouped with other satellite regions rather than adjacent core regions [138]. Dowsett [93] circumvented issues of low or lower species richness in satellite regions by employing Simpson's index [316] to assess 'the proportion of the smaller avifauna that is shared by both' sites. Using this method and the number of endemic species, Dowsett [93] illustrated the relatedness between major montane regions and elucidated the origin and relationships of these species while also noting many transitional and satellite regions.

Similar to Graham *et al.* [138], I find that transitional and satellite regions are often difficult to place and that their position can shift depending on the species being included within the analyses. For many of these sites with low species richness, measures such as nestedness are more effective for elucidating biogeographic relationships, especially when algorithms group clusters together based on absences rather than presences [93]. In his 1986 manuscript, Dowsett [93] recognized seven major montane regions: the Cameroon Highlands, Angola, the Southeastern (including the Southern Great Escarpment north to southern Malawi and central Mozambique), Tanganyika-Nyasa (the southern Eastern Arc and northern Malawi), East Congo (*i.e.* the Lacustrine Rift), Kenya (from the Imatong Mountains to northeastern Tanzania), and Ethiopia (Figure 4.1). Dowsett [93] also considered the Usambara Mountains to be intermediary in composition, and refrained from considering them part of either flanking region. Subsequent authors have recognized similar biogeographic regions, with deviances related primarily to the Eastern Arc Mountains, where work post-1986 has resulted in the discovery of multiple new taxa, clarifications of bird distributions, and a finer-scale understanding of regional community structure [31, 75, 115]. Here, I also find support for 7 major regions from the 2021 list dendrograms; however, these lists differ in their lack of recognition of Angola as distinct from other satellite regions, and in the assignation of mountains in East Africa between an Expanded Eastern Arc and Southern Great Escarpment rather than Dowsett's [93] transitional ranges around a Tanganyika-Nyasa group and a Southeastern Group (Figure 4.1).

Performing analyses at multiple hierarchical taxonomic levels provides a clearer understanding of how community structuring varies across temporal scales and across human interpretations of diversity. While the amount of time that contributes to Genus (and sometimes even Subspecific) levels of diversity varies, it serves as a proxy for varying amounts of accrued diversity through time. Assessing levels of Genus and Superspecies allows historical relationships to provide more weight for clustering models, whereas analyses of Group and Subspecies divided populations as finely as possible between individual montane regions to further elucidate recent relationships. The most consistent group number between authors is recovered for the most intermediary hierarchy used, Species, with the highest variability existing for the levels of Genus and Subspecies. However, these group numbers are sensitive to the inclusion or exclusion of taxa, and thus should not be regarded as firm numbers for the existing number of biogeographic regions. UPGMA clustering methods are more consistent in their overall topologies, however, and large agreements for what constitutes a biogeographic region exist between datasets, though the relationships of these major areas is sometimes unclear, especially for the Bowie [45] species list. Furthermore, the inclusion or exclusion of taxa can affect the placement of transitional regions whose makeup is derived from multiple biogeographic regions.

Analyses of community composition using ecostructure are particularly illuminating for relationships between major biogeographic regions, especially for transitional and some satellite regions (Figure 4.5). While relatively depauperate satellite regions are still grouped together, ecostructure allowed for insight into the complex makeup of regions influenced by multiple biogeographic motifs. Regions such as the Taita Hills, located near the often difficult-to-classify Usambara Mountains [93], show complex patterns of relatedness to adjacent biogeographic regions that are occluded by diversity metrics and classical clustering techniques. Furthermore, adjusting levels of k within the structuring algorithm allows for finer and finer scale analyses of biogeographic breaks within particular regions, allowing for easier interpretations of community composition that defy ordinal classification. Results from ecostructure sometimes make it difficult to assign particular ranges to specific biogeographic motifs, but they are be enormously helpful in identifying transition regions of community admixture [367] and more accurately reflect true patterns of non-uniform colonization between montane taxa, as evidenced by genetics and by varying levels of differentiation within single taxa and superspecies [31, 72, 93, 349]. However, this study still cannot clarify the ambiguity regarding the effects of local extinction on species' modern distributions and modern montane communities given that vicariant processes can result in parallel patterns to dispersal (*e.g.*, in the case of *Gypeatus barbatus* in the Ethiopian Highlands and the Southern Great Escarpment) [31, 380].

All of these results taken together help refine our understanding of the connectivity and clustering of mountain ranges, while also illuminating how our understanding of these relationships changes as our knowledge of the birds of the region improves. Using the 2021 list presented herein, I find that the different sections of the Eastern Arc Mountains, widely considered to be limited to Tanzania [52], may be more broadly considered to include all ranges between the Taita Hills of Kenya and the Chimanimani Mountains of Mozambique & Zimbabwe. Broader connections between these East Afromontane regions have been found for other organisms as well, such as for the frog *Hyperolius substriatus* Ahl 1931, which demonstrates connectivity between parts of the southern Malawi-Mozambique highlands (*e.g.*, Mt. Mulanje) and the Eastern Arc highlands of Tanzania [208]. Similarly, different clustering methods suggest different ways of subsetting the Eastern Arc, and a combination of these methods confirms the presence of multiple distinct subregions and transitional flanking regions that parallels other biogeographic assessments within the region [75, 93]. Likewise, connections found between highland regions herein with many colonization routes hypothesized using ecological niche models for other Afromontane birds and plants [2, 72, 349].

Using these three community lists confirms the stability of many relationships between highland regions with differing species lists, while also illustrating how our interpretation of what constitutes a montane community can change how we view biogeographic relationships. Identical statistical analyses using these different lists resulted in a wide range of recommended cluster numbers while also resulting in surprising polytomies and relationship shifts as species were added or removed to the dataset. Most list concurrence is in fine-scale biogeographic assessments, but some larger scale relationships (*i.e.*, Kenya-Tanzania) are also largely recovered by each author. Polytomies exist in every dataset, and may never be fully resolved given the complex nature of colonization and connectivity between montane regions.

Our understanding of species limits and relationships continues to change (*e.g.*, within the avian genus *Zosterops*) [260], and many taxa that are presently considered populations of lowland taxa (*e.g.*, *Sheppardia gunningi alticola* Fjeldså et al. 2000) may eventually be recognized as endemic montane species. Afromontane species distribution knowledge continues to improve as species like *Nesocharis ansorgei* (Hartert, 1899) continue to be found in regions where they were previously overlooked [87, 243]. Thus, just as the results presented herein challenge some of those presented by previous studies, there is little doubt that future studies will further refine our understanding of biogeographic relationships within the Afromontane highlands.

4.6 Acknowledgments

This manuscript was greatly improved by comments from two anonymous reviewers, and from conversations with John M. Bates, John Novembre, A. Townsend Peterson, and Steve Pruett-Jones. I would also like to thank the Committee on Evolutionary for their support during this research.

4.7 Data accessibility statement

All data and codes are available for use by request.

4.8 Ethics statement

This manuscript relies only upon data from cited sources and does not involve any live animals.

Table 4.2: Number of taxon units (*tc*) and number of clusters (*cl*) per list and per taxonomic category, with average clusters listed across groups and lists. Across each group, I also report the standard deviation (*SD*, σ).

Source	**Genus**	**Superspecies**	**Species**	**Group**	**Subspecies**	**Avg. Clusters**
Dowsett [93]	109 tc., 15 cl.	208 tc., 7 cl.	266 tc., 7 cl.	340 tc., 9 cl.	552 tc., 7 cl.	9 cl.
Bowie [45]	124 tc., 9 cl.	252 tc., 6 cl.	315 tc., 6 cl.	400 tc., 6 cl.	654 tc., 7 cl.	6.8 cl
2021 list	133 tc., 9 cl.	292 tc., 9 cl.	359 tc., 6 cl.	453 tc., 6 cl.	764 tc., 11 cl.	8.2 cl.
Avg. cl. (SD)	11.00 (3.46)	7.33 (1.53)	6.33 (0.58)	7.00 (1.73)	8.33 (2.31)	8.00 (1.11)

CHAPTER 5

GENETIC STRUCTURE, COMPARATIVE NICHE MODELING INFORM CONSERVATION PRIORITIES IN LACUSTRINE RIFT BIRDS

5.1 Abstract

The Lacustrine Rift is one of the most biodiverse regions in Africa, hosting large blocks of Afromontane forest in multiple separate mountain ranges. As the climate continues to change, species' distributions will likewise shift with the possibility for local extinction. In order to address how local extinction may affect genetic diversity of Afromontane birds, we obtained genetic data form sites across the Lacustrine Rift for twelve study taxa. These species ranged from locally endemic taxa (*Graueria vittata*) to more widespread Afromontane species (*Iduna similis*). We created phylogenetic trees and haplotype networks from 3 mitochondrial and 1 nuclear gene for all species to understand the species' phylogeographic structure and biogeographic history. These genetic analyses were complemented with species distribution models to predict the past, current, and future distributions under several different climate change scenarios. Species varied widely in their amounts of genetic diversity and geographic structure, but several patterns emerged from the data. The central Lacustrine Rift, from the Rwenzori Mountains to the Itombwe Highlands, exhibits strong patterns of connectivity, though many species possess regional diversification between the Eastern and Western Rift and even individual montane blocks. The most southerly region included in this study, Mt. Kabobo, was found to be significantly more distinct than has been previously recognized. We show minimal losses of genetic diversity due to climate change within the region, with the caveat that extreme climate change increases the probability of species and subspecies-level extinctions on Mt. Kabobo and in the Mahale Mountains.

5.2 Introduction

Mountains have long been seen as sources of biodiversity, especially in Africa [113, 273, 287]. Climatic cycles connected disjunct montane areas sporadically through history, allowing for populations to mix between or invade into formerly isolated habitats [45, 113, 355]. These dynamics are visible in the present time in areas in Southern Africa and Central Africa where cooler, wetter habitats in specific geographic regions allow otherwise montane faunas to occur regularly at elevations as low as sea level [45, 275, 308]. These climatic cycles have resulted in Afromontane bird populations being widespread but patchily distributed across the continent, with some montane populations being separated by thousands of kilometers across the Congo Basin [317]. These dynamics have led to large-scale diversification of birds continentally and regionally, as in the Eastern Arc mountains, where mountains that are relatively close geographically have allowed for rampant diversification and given rise to endemic taxa restricted to single massifs [46, 49, 52, 260, 353].

The Lacustrine (*i.e.*, Albertine) Rift, a group of highland areas and mountain regions stretching from the shores of Tanganyika in northern Zambia to the shores of Lake Mwitanzige (also known as Lake Albert) on the upper White Nile (Figure 5.1), is home to over a thousand species of bird, of which *c.* 40 species and numerous more subspecies are endemic [272]. This area has been heavily impacted by anthropogenic disturbance, with highland areas being nearly completely deforested except for protected areas [30, 76, 114]. Recent research on the biota of the Lacustrine Rift has predicted range contractions as climate change continues, with species being pushed higher into the montane regions, but has also suggested that suitable habitat corridors will persist between habitat patches for species to access these climatic refugia [11, 13, 274]. Rather, this process of climatic cycling produces an opposite effect, in that climatic cycling builds biodiversity through isolation (similar to insular taxon cycling) [112, 296] as is demonstrated by contemporary bird distributions [275].

Despite significant studies of Lacustrine Rift biodiversity, few studies exist on the history of range shifts and how these shifts have manifested in modern genetic diversity. A study on

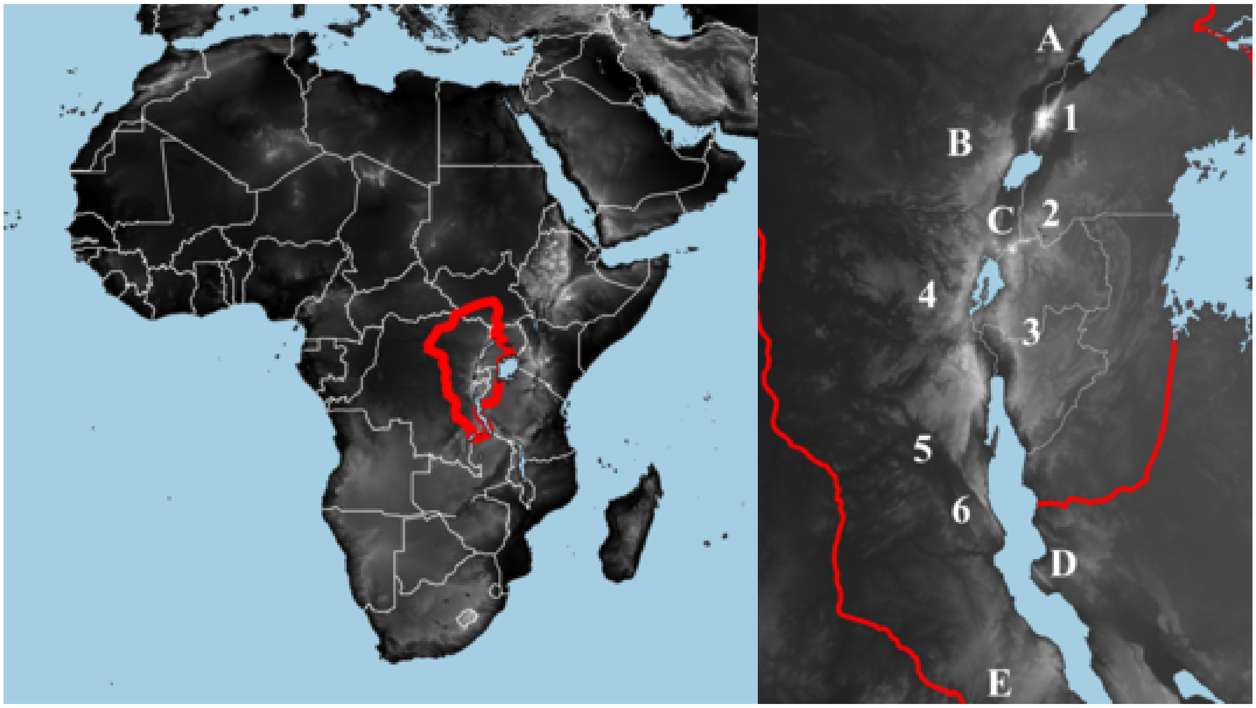

Figure 5.1: Topographic map of Africa, with a black-to-white gradient of 0-4000+ m. Left: The Lacustrine Rift region (red line) within Africa (countries denoted by thin white lines). Right: Inset of the Lacustrine Rift, with specific highlands mentioned within this study. Major study regions numbered and other subregions discussed, lettered. 1: Rwenzori Mountains; 2: Bwindi Highlands; 3: Kibira-Nyungwe Highlands; 4: Kahuzi-Biega Highlands; 5: Itombwe Plateau; 6: Mt. Kabobo. A: Lendu Plateau; B: Highlands west of Lake Rutanzige; C: Central Volcanoes (Nyamuragira, Nyiragongo, Mikeno, Karisimbi, Bisoke, Sabyinyo, Gahinga); D: Mahale Mountains; E: Marungu Highlands.

the swamp-dwelling Grauer's Rush-Warbler *Bradypterus graueri* found that watershed was more important than montane region for phylogenetic diversity, suggesting that montane areas with suitable climatic conditions existing between them may not be enough to foster dispersal and admixture in Lacustrine Rift bird populations [169, 192]. Many Lacustrine Rift taxa are considered polytypic, suggesting that movement between montane regions may be less extensive than is theorized by conservationists. Several of these local subspecies appear to be concentrated in specific areas that may be reflected by genetic data as well, such as the isolated Mt. Kabobo on the eastern shores of Lake Tanganyika, which presently has only one recognized endemic taxon (Kabobo Apalis *Apalis kaboboensis*), but multiple endemic subspecies (*e.g.*, Kabobo Turaco *Ruwenzorornis johnstoni bredoi*) [31]. Other regions possessing endemic species (such as the Western Rift, Democratic Republic of the Congo) have pan-Lacustrine species that are considered undifferentiated from populations in other parts of the Rift Valley (*e.g.*, Northern Double-collared Sunbird *Cinnyris reichenowi* sensu lato) based on morphology [72].

Furthermore, morphological traits often associated with dispersal, such as the Hand-Wing Index (also known as Kipp's Index) [200], have not been found to be reliable predictors of range dynamics in some Lacustrine Rift species[345]. Afromontane species that occur across broad montane areas can exhibit genetic structure between geographically proximate and phenotypically similar populations [72, 353], highlighting the importance of genetic information for understanding population dynamics and connectivity in East Africa [190, 191].

Given the presence of multiple large biogeographic barriers within the Lacustrine Rift and the concordance of many subspecific distributions across the region (see Chapter 3), we hypothesize that many biogeographic barriers will be shared between taxa. Furthermore, we hypothesize that the isolated Mt. Kabobo—which hosts a plethora of endemic taxa—will likely be the most biogeographically unique site within the Lacustrine Rift. We also use our framework to test current taxonomy (and therefore current hypotheses of taxonomic relationships) to determine if partitions based on morphological variation accurately reflect genetic partitions within the region.

5.3 Methods

5.3.1 Study area and study species

In order to assess how past climate change is related to diversity in the Lacustrine Rift, we performed extensive phylogeographic analyses of twelve bird species (Table C.1) and focused on six major montane regions in the Lacustrine Rift, listed here from northeast to southwest: the Rwenzori Mountains, a fault block system reaching 5,109 m on the Democratic Republic of the Congo (DRC)-Uganda border [22]; the Bwindi Highlands of southwestern Uganda; the Kibira-Nyungwe Highlands in Rwanda and Burundi (referred to as the Congo-Nile Divide by Wildlife Conservation Society [327]); the Kahuzi-Biega Highlands in the eastern DRC; Itombwe Highlands in eastern DRC; and the Kabobo (= Kabogo) Forest on the western shores of Lake Tanganyika, DRC (Figure 5.1). We also included samples from other montane regions when available, making specific note of samples from the volcanoes north of Lake Kivu and the highlands west of Lakes Mwitanzige and Rutanzige.

Our focal species range from being localized endemics to widespread montane East African taxa, which we alternatively refer to by the denoted four letter codes: Rwenzori Batis *Batis diops* (BADI; monotypic), endemic to the Lacustrine Rift; White-browed Crombec *Sylvietta leucophrys* (SYLE), with the nominate subspecies in the Lacustrine Rift, *chloronota* in the Rwenzori Mountains east to the Kenyan Highlands, and excluding the Lendu Plateau (west of Lake Mwitanzige) *chapini* which is sometimes granted species status [109]; Grauer's Warbler *Graueria vittata* (GRVI; monotypic), endemic to the central Lacustrine Rift; Rwenzori Apalis *Oreolais ruwenzorii* (ORRU; monotypic), endemic to the Lacustrine Rift; Mountain Yellow-Warbler *Iduna similis* (IDSI; monotypic), found in the Lacustrine Rift and East Africa from South Sudan to Malawi; Red-faced Woodland-Warbler

Phylloscopus laetus (PHLA), with a widespread Lacustrine Rift nominate form and *schoutedeni* from Mt. Kabobo; Rwenzori Hill Babbler *Sylvia atriceps* (SYAT; monotypic) found in the Lacustrine Rift and disjunctly in the Bamenda Highlands of Cameroon; Archer's Robin-Chat *Cossypha archeri* (COAR), with a widespread nominate throughout the Lacustrine Rift and *kimbutui* from Mt. Kabobo; Red-throated Alethe *Chamaetylas poliophrys* (CHPO), with a nominate form throughout the Lacustrine Rift and *kaboboensis* from Mt. Kabobo; Blue-headed Sunbird *Cyanomitra alinae* (CYAL) with a nominate form from Uganda and Rwanda, *tanganjicae* from Kibira-Nyungwe and Kahuzi-Biega, *kaboboensis* from Mt. Kabobo, and the unsampled populations of *derooi* from Lendu, DRC and *marungensis* from Marungu, DRC; Regal Sunbird *Cinnyris regius* (CIRE), with an Lacustrine Rift-wide nominate and the unsampled *anderseni* in Kungwe-Mahale, Tanzania; and Strange Weaver *Ploceus alienus* (PLAL; monotypic) endemic to the Lacustrine Rift. Individual species coverage in relation to the geographic study area is elucidated in Table 5.1; every species that occurs in the Rwenzori Mountains, the Bwindi Highlands, the Kibira-Nyungwe Highlands, and the Kahuzi-Biega Highlands was represented by genetic samples in our study.

5.3.2 Genetic sequencing and processing

We extracted tissue and toepad samples from the American Museum of Natural History and the Field Museum collections at the Pritzker Laboratory for Molecular Systematics and Evolution at the Field Museum. Extractions were performed using a Qiagen DNeasy extraction kit and followed standard protocols. A complete list of samples used can be found in Table C.1. We sequenced different genes for different species, experiencing various amounts of luck with processing samples of different ages from different sources (i.e. tissues vs. toepads), but focused on the mitochondrial genes ATP synthase F_0 subunit 6 (ATP6), cytochrome b (CytB), NADH dehydrogenase 2 (ND2), and NADH dehydrogenase 3 (ND3). Additionally, we sequenced the nuclear genes β-Fibrinogen 5 and Transforming growth factor-β2 (TGF-β2). A complete gene coverage matrix is shown in Table 5.2. We performed all sequencing using the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California). We precipitated sequencing reactions with ethanol and 125mM EDTA, running samples on an ABI 3730 DNA Analyzer.

Sequences were imported to Geneious 9.1.8 (`http://www.geneious.com`), concatenated by individual, and then aligned by species. We used default Geneious alignment methods, and exported alignments as phylip and nexus files for subsequent downstream analyses. For taxa that possessed large amounts of missing bases (*i.e.*, IDSI, ORRU, PHLA, and SYAT), we created a secondary concatenated file with large missing sections removed for haplonet analyses.

5.3.3 Genetic analyses

Using PopART 1.7, we created median-joining networks of populations to view major regional structure in each species [14, 209]. We used these networks to identify major genetic clusters and see their geographic makeup. This enabled us to observe how admixed geographic regions are with respect to genetic lineages. For species that had large amounts of missing data (*i.e.*, IDSI, ORRU, PHLA, and SYAT), we deleted poorly represented regions to improve PopART's ability to assign individuals to unique populations (adjusted sequences available in supplementary data).

We imported available mitochondrial genes to **BEAST** v. 2.5 [44] to create a time-calibrated phylogeny. We used a strict clock model with a normal distribution rate, using the substitution rates and 95% highest posterior density (HPD; in parentheses) of the substitutions per site per lineage per million years (s/s/l/myr) reported by [211]: ATP6 0.026 (0.021-0.031) s/s/l/myr; ND2 0.029 (0.024-0.033) s/s/l/myr; and ND3 0.024 (0.018-0.031) s/s/l/myr. Estimated divergence rates between different species of oscine passerines are similar, and these rates have been used in multiple other studies of tropical birds [192, 363]. We created a single linked tree using all available mitochondrial genes, with clocks adjusted independently for each gene in **BEAST** v. 2.5 [44]. Runs were 10 million generations in length, saving every 1,000 generations and considering the first 10 thousand runs as burn in. Outputs were viewed in **Tracer** 1.7 [289]. Most analyses showed a stable trace by the end of the run, but we refrained from individually changing parameters to maintain the uniformity of the analyses for each taxon. Phylogenetic trees were concatenated in *LogCombiner* and annotated with *TreeAnnotator*, included in the **BEAST** 2.5 installation [44], before being viewed in **FigTree** (`http://tree.bio.ed.ac.uk/software/figtree/`). We also created phylogenetic hypotheses using all available genes and **RaxML-SSE3** [330] using a GTRGAMMA model and a random seed of 19877 before determining support with a run of 7175 bootstraps. We used **RaxML** to create a 'best' hypothesis of topology between individuals and major phylogeographic groups [330]. Using a custom code in **R** 3.6.3 [285] and the **R** package *phytools* [295], we calculated gross genetic sequence divergence in genomes between populations to further compare observed diversification (see Appendix).

5.3.4 Data preparation

We followed the general pipeline of Strimas-Mackey [332], with alterations to suit our data requirements and processing needs. All steps were performed in **R** 3.6.3 [285], using the general data management packages of *data.table* [92] and *tidyverse* [370]. Our entire code is available in the supplementary information, and we summarize our general pipeline here.

Specimen and observation data (excluding the eBird database; see below) were downloaded via the Global Biodiversity Informatics Facility (GBIF) on 9-10 October 2019 [131–133]. We plotted each dataset independently to determine whether or not data are gridded or inaccurately plotted from the raw database. Gridded data were removed, as their spatial uncertainty can not be assessed as precisely as point-based data, and because gridded data may not align with the weather data layers that are being used, thereby biasing the data. A complete list of institutions contributing to the GBIF dataset is available via the GBIF download DOIs. Using a similar process to the eBird data, GBIF data were vetted for inconsistencies, and points were removed as follows: BADI (1 point); CHPO (1 point); CYAL

(1 point); GRVI (2 points); ORRU (4 points); and SYLE (1 point). GBIF derived data were combined with the previously downloaded eBird data, and additional files were created of 'historic' records (predominately specimens from before 2009) and 'modern' records (predominately eBird records from 2009 onwards). The choice of this date was in part because of the proliferation of eBird data and in part due to the availability of landcover data for ecological niche modeling.

We downloaded the eBird dataset 'ebd_relAug-2019' [97] directly from eBird [334], and extracted data for our study species individually using the R package *auk* [333]. Files were then reduced in size by deleting extraneous columns and reformatted (using the package *lubridate* [149] for downstream analysis. eBird data were limited to efforts of less than or equal to 5 km, less than or equal to five hours, and with 10 or fewer observers [332]. Spatial checks were performed by overlaying the data with maps of the region using the **R** packages *sf* [261] and *rnaturalearth* [328] and comparing data to published distributions [57, 60–62, 64–66, 80, 218, 257–259, 304, 317, 331]. Points that were from habitats where the species are not known, had ambiguous locality data, or appeared to be incorrectly plotted in general were removed. eBird occurrence datasets for several species were not altered; three localities were removed from CYAL, two from CIRE, and one apiece from COAR, IDSI, ORRU, PHLA, PLAL, SYAT, and SYLE, almost all of which are from the vicinity of Lake Mburu, Uganda which is a lowland site outside the ranges of these species.

We created two sets of niche models using two different methodologies, for a total of four sets of niche models, to understand how species' distributions shift with relation to climate. The two methods implemented were a random forest (machine learning) approach outlined in the eBird best practices pipeline [332], and the second method was a custom pipeline using minimum volume ellipsoids (MVEs; custom code adapted from J. Soberón) [347] to create presence-only models [72]. We opted for using both methodologies to compare how these methodologies predict current and past distributions. Within each method, the first set of models used the ENVIREM dataset [339] in combination with the Normalized Difference

Vegetation Index (NDVI) accessed from the MODIS database using the **R** packages *hdf5r* [164] and *modis* [234]. We specifically used the ENVIREM layers of the Thornthwaite aridity index (measuring the degree of water deficit), continentality (difference between the average temperature of the warmest and coldest months), Emberger's pluviothermic quotient (differentiating between Mediterranean climate types), the maximum temperature of the coldest month, the minimum temperature of the warmest month, the precipitation of the driest quarter, and the precipitation of the wettest quarter. These environmental variables have been shown to be important for other bird species, including those found in Afromontane landscapes [72, 73, 302].

In addition to the aforementioned **R** packages, we also used *raster* [157], *rgdal* [35], *gdalUtils* [145], and *velox* [172] to manipulate data and extract environmental variables for specific localities, using a code based on that put forth in the eBird best practices pipeline [332]. Each model was restricted to a biogeographic training area specifically designed for that species in order to reflect how biogeographic historic has limited species distributions [73, 255, 325]. We downloaded NDVI data from 2009-2019, and created an annual raster of the maximum and minimum NDVI file for each individual grid cell, and corrected all grids to have the same resolution and spatial extent (30”, or *c.* 1 km at the Equator). No size correction for cells was made as the study is wholly restricted to the tropics, and size distortion within the study area is not extreme [73]. The joint NDVI and ENVIREM models were created using only the modern data that could be aligned temporally with the appropriate MODIS data layers.

The second set of niche models was created using WorldClim v 1.4 (Hijmans et al. 2005). In order to have variables align with the ENVIREM dataset, we manually created the data layers of the Thornthwaite aridity index, continentality, and Emberger's pluviothermic quotient using the R package *envirem* [339] and available WorldClim layers. We combined these layers with the mean temperature of the warmest quarter (BIO10), the mean temperature of the coldest quarter (BIO11), the precipitation of the driest quarter (BIO17), and the precipitation of the wettest quarter (BIO16). Additionally, we selected three future climate models – CCSM4, GISS-E2-R, ad MIROC-5 – for all Representative Concentration Pathway (RCP) projections available for 2050 and 2070 (RCPs 26, 45, 60 & 85). Past climate data were downloaded for CCSM4, MIROC-ESM, and MPI-MSI-P for the mid-Holocene (*c.* 6 kya) and the Last Glacial Maximum (LGM; ca. 22 kya). We also downloaded a separate dataset of Last Interglacial (LIG; 120-140 kya) data made available through the WorldClim website.

For each species, we created a prediction surface across which models could be projected from the relevant bioclimatic layers to account for spatial inaccuracies and distance traveled during data collection (specifically for eBird checklists) [332]. Prediction surfaces were made by creating new data layers wherein each individual prediction surface raster cell is the average of the given cell and its surrounding raster cells; thus, each prediction surface raster cell is a reflection of the local environmental conditions surrounding the cell and not simply the conditions of the cell itself in the original dataset. Prediction surfaces were employed to account for spatial movements by observers and by the birds themselves, thus accounting for the fact that both groups may be cuing in to environmental characters *near* the observation point and not *at* the observation point (*e.g.*, species encountered traveling between habitat patches). We defined our neighborhood size for calculating prediction surface cell characters as 3 km.

5.3.5 Random Forest modeling

We used a machine learning approach using Random Forests to create our first group of distribution models. We used the **R** packages *dggridR* [16], *ranger* [375], *scam* [280], *PresenceAbsence* [118], *verification* [249], *maptools* [38], *edarf* [189], *ebirdst* [9], *fields* [251], as well as other aforementioned **R** packages. Random Forest models were run 1000 times for each species, using the variable importance metric of ‘impurity’. We did not perform additional model calibrations as many of these calibrations (especially those involving data rarefication) decreased the power of our Random Forest models [332].

5.3.6 Minimum volume ellipsoids

We created a second set of ecological niche models using minimum volume ellipsoids (MVEs) based on presences from throughout the region [347]. MVEs were calculated the **R** packages *MASS* [351] and *ellipse* [247] to create a covariance ellipsoid with a quantile of 0.9, which was then used to project suitability spatially based on the Mahalonobis distance [72, 103, 226] of the points to the niche centroid. These models were performed on the same data layers as the random forest models, but used only species presences and ignored absences.

5.3.7 Post-processing of models

We thresholded our derived distribution models based on thresholds of 100% (e.g., all reported records are correctly referring to localities where the species is regularly found), 90% (*e.g.*, 90% of records are reliable), and 75% [73]. Given that we used a niche modeling method that requires presences and absences, we restricted each species' distribution model to an **M** (*i.e.*, accessible area) that accounts for the biogeographically accessible regions in which the species occurs and for which data exist. We therefore did not model *Iduna similis*, *Sylvia atriceps*, and *Sylvietta leucophrys* on Mt. Kabobo, where the species have been reported but where our dataset downloads did not retrieve any positive occurrence records, to avoid biasing the distribution models for these species in that area [31, 33, 73] When using bioclimatic variables, model suitability was projected onto prediction surfaces for every time period and thresholded using this same methodology. Model outputs using all data points for both historical and modern data were combined for each modeled time period to understand the regions of most likely inhabitation and to understand how models differ. We calculated gross (%) range change in terms of area between these models to understand how much of each species' distribution would be lost through future climate change (or gained if looking backwards through time).

5.4 Results

5.4.1 Biogeographic breaks

Species distribution models generally identified three isolated regions within the Lacustrine Rift: the Rwenzori Mountains; the central rift highlands, including the Eastern and Western regions connected via montane forest in the volcanoes between Lake Rutanzige and Lake Kivu; and the southerly Mt. Kabobo. Genetic variability differed between species, with very little genetic divergence observed in some species (maximum 1.1% sequence divergence between any clades in *Oreolais ruwenzorii*) to larger divergences seen within the same geographic area (*e.g.*, 1.49% sequence divergence between *Graueria vittata* within the Kahuzi-Biega Highlands of the Western Rift). Regardless of how isolated the northernmost sampling site, the Rwenzori Mountains, appears in species distribution models, populations from these mountains frequently shared haplotypes with populations to the south. Most species showed strong connections between the Rwenzori Mountains and the eastern highlands of Bwindi and Kibira-Nyungwe. Even in species where Rwenzori Mountains populations were fairly divergent (*e.g.*, *Cinnyris regius*), some Rwenzori individuals fell into clades that are predominant in other montane regions on both sides of the rift, indicating either recent migration or incomplete lineage sorting between these populations. In *Oreolais ruwenzorii*, Rwenzori haplotypes clustered with samples from Kahuzi-Biega on the western side of the rift, with these mountain ranges being sister to other highlands in the eastern rift; this pattern was not found in any other species, but is indicative of a complex pattern of intermontane differentiation/colonization in Lacustrine Rift bird species.

Species responses to biogeographic breaks varied greatly. *Phylloscopus laetus* possesses its highest genetic divergence (up to 1.16%) within a single population (Mt. Kabobo, described as subspecies *schoutedeni*) and little evidence for regional monophyly anywhere within its range (Figure C.6) [62]. Conversely, *Cossypha archeri* possesses the largest amount of regional diversification, with clear geographic structure and 7.07% sequence divergence between the Mt. Kabobo and the Western Rift (Figure C.8). Individual species histories shared little with regards to timing of divergences, and were instead limited to geographic similarities in where population breaks occur (Figures C.13-C.24).

5.4.2 Population structure

Species can largely be broken into three main groups based on genetics:

1. species that possess deep divergences between at least two biogeographic areas;
2. species that possess lesser amounts of regional diversification with phylogenetic diversity suggesting migration; and
3. species with varying amounts of diversity and weak geographic structure (Figure 5.2).

Our models do not predict regional extinction for any haplotype groups within this study in the near future.

Deep diversification events Mount Kabobo was frequently recovered as a unique geographic region with respect to genetic structure. Four taxa (BADI, COAR, CYAL, PHLA) have divergence dates of > 250 kya for the divergence for Mt. Kabobo lineages. Only one of these species (*Phylloscopus laetus*) showed evidence of haplotype sharing between Mt. Kabobo and other geographic areas (Figure C.18); all other taxa were reciprocally monophyletic. Two of these deeply diverging species have described subspecies from Mt. Kabobo: *Cossypha archeri kimbutui* (isolated 1.13-1.16 mya from other rift populations; Figure C.8, C.20) and *Cyanomitra alinae kaboboensis* (isolated 568-907 kya from other sampled populations; Figure 5.2, C.22). Another species with described phenotypic variation, *Chamaetylas poliophrys*, also possesses an endemic subspecies on Mt. Kabobo (*kaboboensis*) that is reciprocally monophyletic and has been isolated for 176-364 kya (Figure C.9, C.21). The Mt. Kabobo population of *Sylvietta leucophrys*, represented by a single sample, appears to have

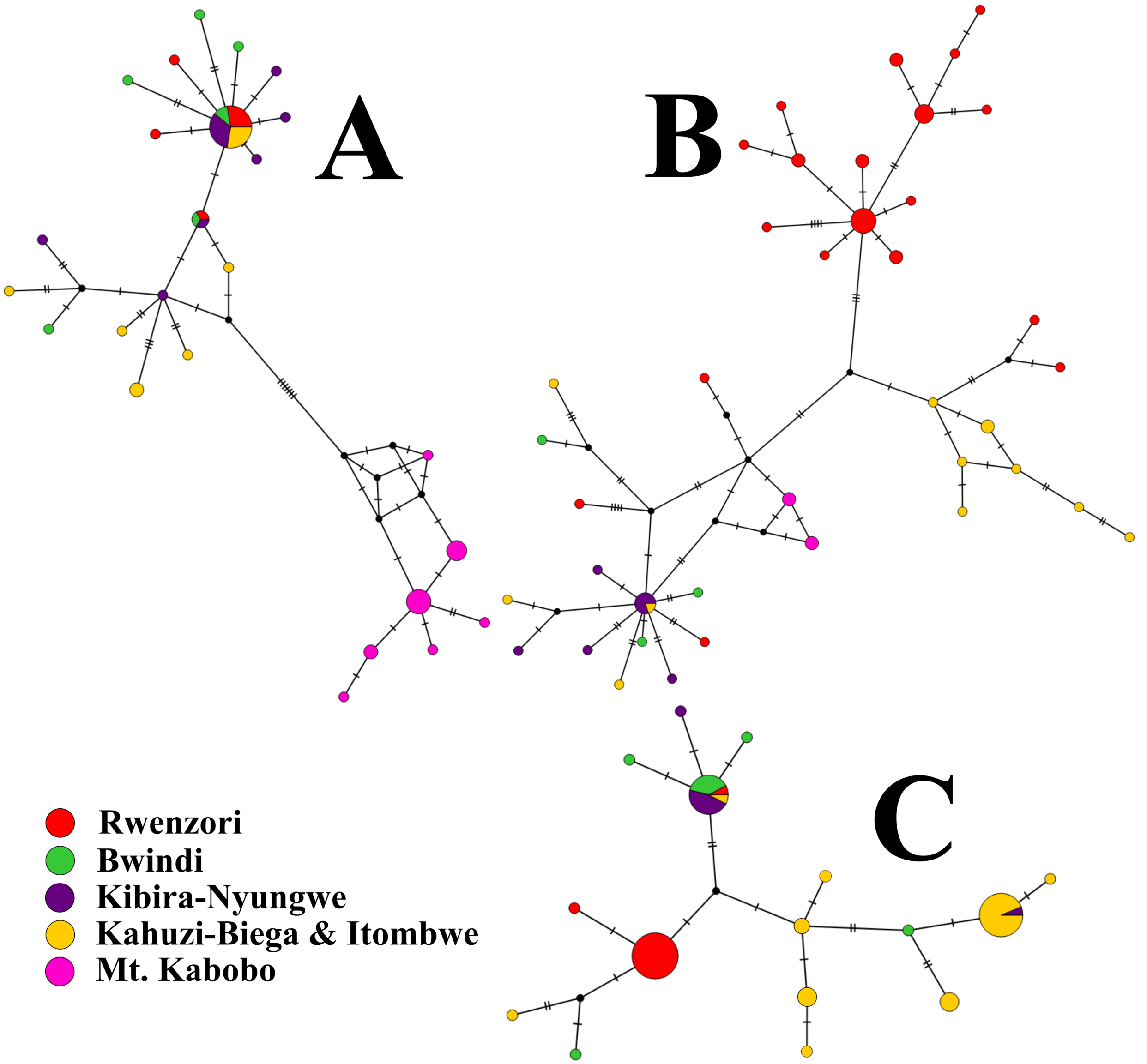

Figure 5.2: Haplotype networks illustrating the three major diversification patterns found within the Lacustrine Rift: A) Notably high divergences between Mt. Kabobo and the main rift (*Chamaetylas poliophrys* complex, ND2); B) Regional diversification between major montane blocks with evidence on gene flow (*Cinnyris regius*, ND2); and C) low levels of diversification with evidence for repeated genetic interchange between montane blocks (*Sylvia atriceps*, ND2). Networks are not to scale.

been isolated for 134-268 kya; however, this species also possesses an equally divergent lineage embedded within other haplotype groups in the Kibira-Nyungwe highlands and has no described geographic variation from the southern Lacustrine Rift (Figure C.14).

Regional diversification and diversification with gene flow Varying levels of diversification were observed between major geographic areas, with diversification events between lineages as old as 405-640 kya (*Sylvia atriceps* between the East and West Lacustrine Rift; Figure 5.2, C.19). However, most of these species showed evidence of recent migration between geographic regions. Many species had surprising levels of diversity intermixed within geographic areas, such as the aforementioned *Sylvietta leucophrys* (Figures C.2, C.14). *Phylloscopus laetus* shows large amounts amounts of haplotype shaping between divergent lineages, with the population almost appearing panmictic despite lineage divergence events as old as 315-535 kya (Figures C.6, C.18). Other species demonstrated clearer phylogeographic breaks, such as *Batis diops*, but still had some evidence of gene flow between some populations (in this instance, one individual of the western group having an wastern haplotype; Figures C.1, C.13).

Low diversity with geographic structure Some taxa (*i.e.*, *Cinnyris regius*) possess regional genetic lineages (*i.e.*, mostly Rwenzori, mostly Kahuzi-Biega) with each of these geographic areas possessing some haplotype sharing with other regions (Figure 5.2). These species consistently showed low levels of diversification between the Eastern Rift (Bwindi and Kibira-Nyungwe), the Rwenzori Mountains, and the Western Rift (Kahuzi-Biega and Itombwe). This pattern includes one species with divergent populations from Mt. Kabobo (*Cyanomitra alinae*) but no structure across other sites (Figure C.10, C.22).

5.4.3 Range dynamics

We report our niche modeling results using 90% confidence models, as these reflect a general confidence level in the data and these models more closely resemble described distributions than relatively over-fit 75% threshold models and relatively under-fit 100% threshold models. For all models, ENVIREM-based predictions possessed lower predictions away from montane zones, and were more concisely limited to highland montane areas. Because ENVIREM models also included MODIS NDVI data, they also had higher predictions in most forested montane areas. The high interior parts of the Rwenzori Mountains, for example, possessed fairly high predictions despite the regions being (currently) inhospitable to lower elevation forest taxa. Conversely, WorldClim models appeared to do a better job of limiting species to narrow elevation bands within the mountains. While this improved predictions in the eastern rift, it often did a poorer job of representing species in the western rift (eastern Democratic Republic of Congo).

The area of predicted occurrence varied widely with respect to the method used (MVE vs. Random Forest) and with respect to the variables used (NDVI data vs. BIOCLIM only). For Random Forest datasets, the area predicted to be suitable by both models was found to be less than the combination of the areas from each of them (average 66.7% reduction for all species; range 43.1-86.2%; Table S2 online). Reductions in occupied area varied by year and by predicted RCP level; by all metrics, the range of all species was less in 2070 than in 2050 (average reductions of 76.6% reduction and 67.9% reduction in range size compared to present, respectively). Ranges do appear to shift towards higher elevations, with higher elevation areas of absence in-filling as ranges retract in lower elevations. Models of several species included areas of predicted occurrence from areas where the species is not known; these errors are due to habitats that are similar enough with respect to climate or forest cover to warrant inclusion in the finalized models based off of our threshold criteria.

For minimum volume ellipsoid models, all ranges were predicted to be much smaller than when using Random Forest models. This is most notable in species such as *Sylvia atriceps*, where no ‘stable’ areas were recovered for 2050 or 2070, suggesting that populations will have to move to new areas of suitability to persist, contra the Random Forest models that recover 799 km2 and 539 km2 of stable habitat through these time periods, respectively. Range losses were predicted to be much larger using MVE models, with average range contractions of 80.0% for 2050 and 89.6% for 2070.

Random Forest and MVE models differed dramatically with respect to historical distributions. This difference was perhaps most notable in past climates, where MVE models predicted no stable areas of occupancy for any species except for *Iduna similis* (93.4 km^2). Random Forest models found stable areas for all models through all time periods, with the smallest area of distribution stability for past models being 38.8 km^2 for *Graueria vittata* and the largest stable area being 45,162 km^2 for *Cinnyris regius*. Using random forest models, almost all species showed broader distributions with larger amounts of connectivity between Lacustrine Rift highlands, with only two currently occupied mountain ranges consistently retaining their isolation: the Rwenzori Mountains and Mt. Kabobo.

Through all time windows, the ranges of these species vary widely. 'Ghost' populations in areas of suitability that theoretically existed for many species appear in outlying areas, and almost all Eastern and Western Rift regions show connectivity in past climactic models. Within the study area, only two regions – the Rwenzori Mountains and Mt. Kabobo – maintain their spatial isolation through all time periods. For those species that do appear in the Lendu Plateau (*i.e.*, the northwesternmost edge of the Lacustrine Rift), this region appears to be isolated through all time periods as well. Several models show strange patterns of occurrence in the Congo Basin itself in past and future climate models; the patterns of these distributions appear to be artefactual and a reflection of the way in which environmental data layers are created for these regions (but see discussion).

While we do not predict the losses of any major genetic group, we do predict local extinctions or near-extinctions for *Sylvia atriceps* on Mt. Kabobo (a population not sequenced herein; Figures C.43, C.55). We also predict a severe range constriction for *Cossypha archeri kimbutui* on Mt. Kabobo (Figures 5.3, C.56), *Iduna similis* throughout the Lacustrine Rift (Figures C.43, C.53), and *Cinnyris regius anderseni* in the Mahale Mountains of Tanzania, an extralimital population that was not sequenced for this study (Figures C.47, C.59).

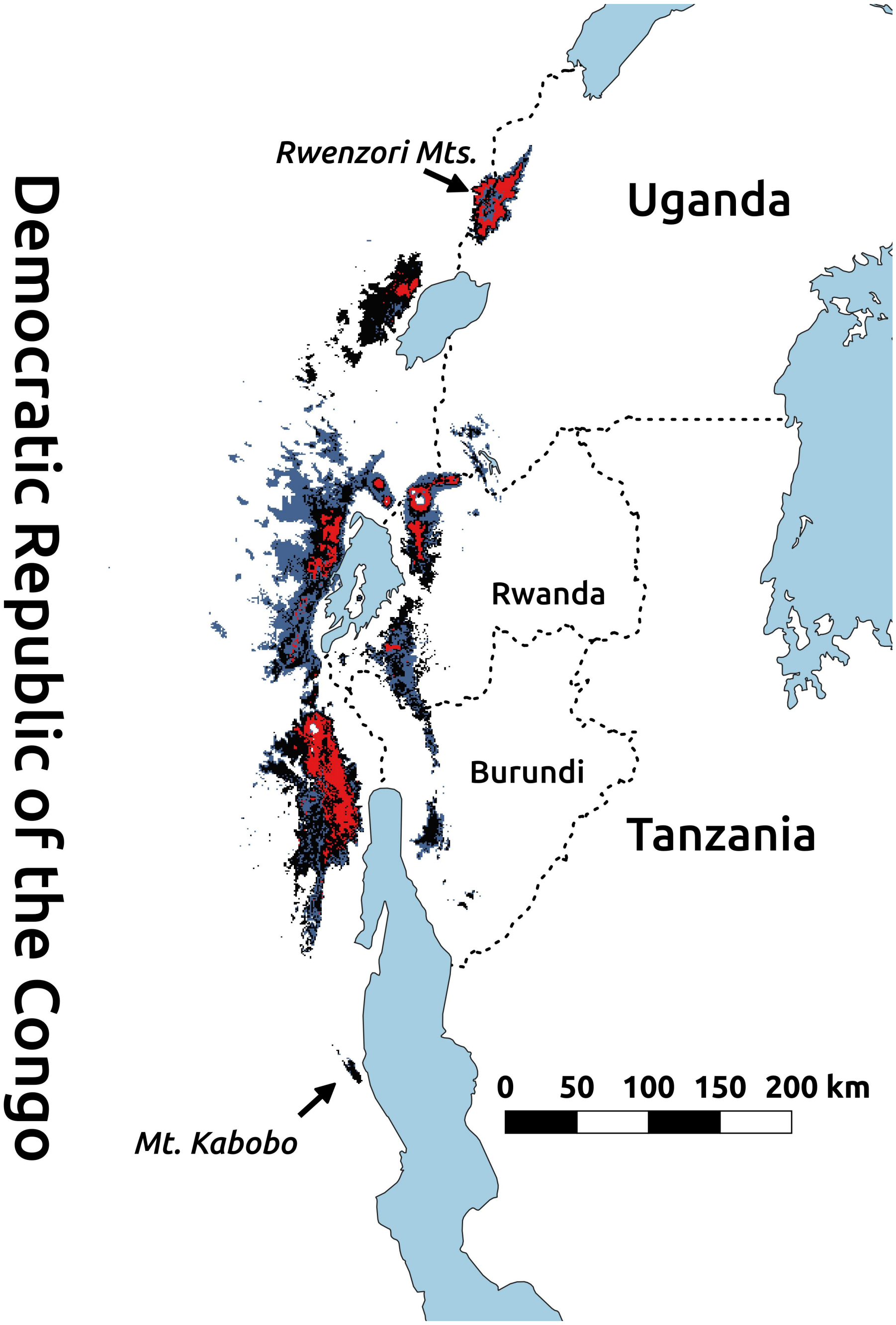

Figure 5.3: Past (dark blue), present (black), and future (red) distribution estimates for *Cossypha archeri*, including *Cossypha kimbutui* (restricted to Mt. Kabobo). Map is of the Lacustrine Rift (with north at the top of the image), with the northernmost (Rwenzori Mts.) and southernmost (Mt. Kabobo) study sites marked, with lakes shown in light blue and contemporary country borders shown with dashed lines. Map created using the Random Forest pipeline.

5.5 Discussion

Our genetic analyses confirm that Lacustrine Rift montane birds can and do maintain connectivity across some subregions in some species. The most distinctive region from a genetic perspective is Mt. Kabobo (5/12 with divergent and reciprocally monophyletic lineages), which is also one of the most geographically isolated montane regions, whereas our results suggest large amounts of connectivity between all other Lacustrine Rift regions for most species. These results are mirrored by niche modelling of historical climate which supports connectivity of highland forests during the last glacial maximum. Our ecological niche models demonstrate reductions in the occupied area into the present for all species, but that the amount of reduction in the species ranges is 'fixed' within the modeled time period by the amount of invasible habitat at higher elevations. Our models do not discount that migration between populations is possible as the climate changes, and that maintaining protected areas and habitat corridors will help facilitate connectivity in these species [13]. Varied genetic landscapes for each species are perhaps indicative of differential abilities for species to cope with biogeographic barriers within the region [54]. These different abilities in dispersal manifest themselves in some dramatic ways, with one species (*Batis diops*) demonstrating clear genetic divergence between the Eastern and Western Rift despite occasional connectivity in the modern era. Thus, taxa within the region are experiencing clear genetic differentiation with ongoing gene flow.

Despite theoretical advantages to using presence-only minimum volume ellipsoids, we find better translation through time (*i.e.*, recover realistic estimates of suitability) for Random Forest models [72, 254]. The reason may reflect an overfitting of MVE models to current climatic conditions [102]. MVE's performed extremely poorly when projecting backwards through time (predicting stable suitable areas for only two species during past climates where Random Forests found suitable areas for every species), but on average predicted larger range sizes for species in the present day. This disagreements illustrate the utility of comparing different modeling methods for different species and different time periods.

5.5.1 Climate change and genetic diversity

The historical geographic patterns between connectivity and isolation in Lacustrine Rift birds is apparent from their genetic diversity. Perhaps the most striking example is *Phylloscopus laetus*, where mitochondrial lineage divergences of up to *c.* 430 kya co-occur in birds sampled from the same highland (Figure C.18). There are only two subspecies of *Phylloscopus laetus* described, with the endemic *schoutedeni* from the Lacustrine Rift genetically encapsulating most of the diversity observed within the species as a whole, and potentially indicative of a large effective population size through time or a population robust to habitat (and associated population) fragmentation [56]. Other taxa, namely *Sylvietta leucophrys*, have divergent genetic lineages that are represented by few samples, and are perhaps snapshots to diversification events that have since been overwhelmed and virtually wiped out by more recent connectivity and population sizes that are insufficient for maintaining historic genetic diversity.

Populations separated across by biogeographic breaks do possess genetic signatures that are especially evident in haplotype networks, but for most species there is ongoing evidence of gene flow between montane regions. Based on historic niche models, the northernmost highlands, the Rwenzori Mountains and the Lendu Plateau, and the southernmost highland, Mt. Kabobo, show evidence of long term isolation, but only Mt. Kabobo possesses multiple reciprocally monophyletic, phenotypically distinct populations. More research is required to understand how the spatially smaller gap between the Itombwe Plateau and Mt. Kabobo is a greater biogeographic barrier for most species than the lowlands of the northern Lacustrine Rift. The geology of the region likely plays an important and potentially complex role in aspects of these patterns. In the center of the entire region are a set of recent, still active volcanoes (the Virungas) between Lakes Kivu and Rutanzige, that form a highland area that lies geographically between the Bwindi highlands of the Eastern Rift and the Western Rift. Parts of the Virungas share some endemic species with the Western Rift that are apparently absent in the Eastern Rift (*e.g.*, *Prionops alberti*; `https://ebird.org/checklist/S15374389`); genetic samples from this region would greatly clarify the relationships of birds within this region and shed light on whether the Virungas are currently functioning as a dispersal corridor for montane taxa.

We find no evidence of local extinction from climate change for any major genetic groups within our study species, despite the fact that some local populations are projected to decrease dramatically and potentially go extinct (*e.g.*, Rwenzori populations of *Chamaetylas poliophrys* may disappear, but are genetically the same as other Lacustrine Rift populations). We report this finding with the caveat that we were unable to sample all described subspecies for every lineage: we observe little suitable habitat for *Cinnyris regius anderseni* in the Mahale Mountains of Tanzania, but are cautiously optimistic that the population will be able to persist. We do predict greatly reduced distributions or even local extinctions for populations of *Iduna similis* in Malawi and Tanzania, but predict little loss in genetic diversity given the similarity of genetic sequences between birds in Malawi with those in South Sudan and the Rwenzori Mountains (Figures C.41, C.53). The most endangered genetically distinct populations we recovered are those found on Mt. Kabobo, specifically the robin-chat *Cossypha archeri kimbutui*, a genetically distinct population whose range will dramatically decrease (Figures 5.3, C.8, C.20, C.32, C.44, C.56). More research is required to understand how these isolated, divergent populations will fare, given that many populations have been isolated on Mt. Kabobo long enough for significant evolutionary divergence to occur. These populations may be adapting to local climates, a factor that is not be accounted for in species-complex-wide ecological niche models with limited samples from range-restricted populations.

5.5.2 Revisiting population delimitation

Diagnosable taxonomic units are important for ongoing conservation efforts, and proper species delimitation is critical for allocating conservation resources appropriately [225]. Mount Kabobo is included within the LaLuama-Katanga-Mt. Kabobo important bird area, which is notable for having multiple range restricted species but only one endemic species, *Apalis kaboboensis* [33]. When the area is considered in part with the more southerly Marungu Plateau (sensu the Wildlife Conservation Society), the number of endemic bird species increases to two, with the addition of *Cinnyris prigoginei* [224].

Mount Kabobo has seven described subspecies that are considered endemic to the massif; our study included four of these endemics. We recovered reciprocal monophyly for three of these subspecies: *Cossypha archeri kimbutui*, *Chamaetylas poliophrys kaboboensis*, and *Cyanomitra alinae kaboboensis*. Additionally, we found a well-supported well-differentiated clade of *Batis diops* inhabiting the mountain range, and evidence that local *Sylvietta leucophrys* may also be genetically distinct. The ages of each species' diversification event varied, with the oldest diverging population being *Cossypha archeri kimbutui* at 1.13-1.16 mya (Figure C.20) and the youngest being *Chamaetylas poliophrys* at 176-364 kya (Figure C.21); for all of these populations, uncorrected sequence divergence ranges from 0.961-7.26%. This result is in line with other studies of African phylogeography that have found that species' with similar patterns of geographic distribution do not show congruent timing for evolution divergence events [230, 349]. Only one described subspecies, *Phylloscopus laetus schoutedeni*, showed extensive evidence of gene flow between geographic regions but still possessed a unique Mt. Kabobo haplotype with a divergence time of 316-535 kya (Figure C.18). Given the asynchrony of the timing of events and the lack of congruent timing, it is possible that some species reached Mt. Kabobo via jump-dispersal rather than vicariance from more-distant habitat connectivity. With the exception of *Phylloscopus laetus*, the interaction between ecology, geography, and genetics has been sufficient to maintain separately evolving populations on Mt. Kabobo with respect to other geographic regions in the Lacustrine Rift.

We argue that populations that are distinct with respect to their geography, phenotype, and are genetically monophyletic are best recognized as distinct species based on numerous species definitions including the Evolutionary Species Concept, the Phylogenetic Species

Concept, and the Phenetic Species Concept [283]. Within this study, the three populations that we would suggest should be elevated to species level are all found on the more isolated Mt. Kabobo, an area already recognized for its distinctiveness and isolation with respect to the rest of the Lacustrine Rift, and stand in contrast with other, better dispersing taxa (*e.g.*, *Phylloscopus laetus*, *Cinnyris regius*) that show evidence of ongoing or recent movement between montane blocks. Specifically, the following Mt. Kabobo endemics should be recognized as full species:

Kabobo Robin-Chat *Cossypha kimbutui* (Prigogine, 1955), a monotypic *Cossypha* endemic to Mt. Kabobo, thus rendering *Cossypha archeri* a monotypic species endemic to the main Lacustrine Rift.

Kabobo Alethe *Chamaetylas kaboboensis* (Prigogine, 1957), a monotypic *Chamaetylas* endemic to Mt. Kabobo, thus rendering *Chamaetylas poliophrys* a monotypic endemic to the main Lacustrine Rift.

Kabobo Sunbird *Cyanomitra kaboboensis* (Prigogine, 1975), including the nominate subspecies on Mt. Kabobo and tentatively including the subspecies *marungensis* from the adjacent Marungu Plateau. The subspecies *marungensis* has never been analyzed using genetic sequences, and more research is required to clarify its relationship to *C. k. kaboboensis* and *C. alinae*. Recognizing *C. kaboboensis* would result in *C. alinae* containing three subspecies: *alinae* in the Rwenzori Mountains and the Eastern Rift, *tanganjicae* in the Western Rift and Kibira-Nyungwe, and *derooi* of the Lendu Plateau and surrounding regions.

Given the size of the Mt. Kabobo [33] and the area of occupancy trends we have observed, *Cossypha kimbutui* qualifies as globally Endangered (extent of occurrence $<$2,500 km^2, single site endemic whose area of occupancy is predicted to decline), whereas *Chamaetylas kaboboensis* and *Cyanomitra kaboboensis* are best considered Near Threatened given their broader distributions and less marked population declines [179]. Further research is required to determine the status of Mt. Kabobo's *Batis* populations; while they appear to be distinct per the phylogenetic species concept and some may recognize them as species based on their genetics, field diagnosable features between the populations are also desired, especially since this population is presently lacking a scientific name [359].

We found large amounts of haplotype sharing within several species covered by this study. We find little support for recognizing eastern and western *Cyanomitra alinae* as separate subspecies (*alinae* and *tanganjicae*, respectively), and a review of morphological characters is necessary to determine if these populations should be synonymized. However, *Phylloscopus laetus schoutedeni* appears to represent an example of a differentiated subspecies that has merged with adjacent populations, as it is phenotypically distinct enough to be recognized as a separate entity and it contains unique, highly divergence genetic lineages intermixed with lineages from other montane regions. We find support for most current subspecific assignments in the Lacustrine Rift given our patterns of phylogeographic relationships and the distributions ascribed to these subspecies in the literature. Several phenotypically distinct subspecies not included in this study from peripheral highland areas of the Lacustrine Rift (Figure 5.1), such as *Cinnyris regius anderseni* (Mahale Mountains) and *Sylvietta leucophrys chapini* (Lendu Plateau) require modern sequencing to understand their relationships within their species' complexes.

5.5.3 Evolutionarily guided conservation

Here, using genetic sequences in conjunction with ecological niche models, we have been able to show that the isolation of populations does not necessarily correlate with an inability of populations from different montane regions to remain connected. The Rwenzori Mountains are consistently grouped with other mountain ranges within the Lacustrine Rift, whereas the similarly geographically isolated Mt. Kabobo is consistently found to be a distinct biogeographic region. Moreover, we find 4-5 Mt. Kabobo populations should be recognized as species, endemic to the Kabobo region increasing avian species diversity of this highland fourfold.

While interbreeding appears to be promoting cohesiveness among populations in the

Lacustrine Rift, it is important to note that specific regions have unique haplotypes or vary in the proportions of genetic diversity they preserve. It is not uncommon for montane areas (such as the Rwenzori Mountains) to possess unique haplotypes, despite the fact that multiple haplotypes are found within the mountain range. Regional diversification is ongoing in Lacustrine Rift birds, and conservation of populations in all major geographic regions is important to preserve the modern diversity of these taxa.

For many species, the Eastern Rift (specifically the highlands of Kibira-Nyungwe and Bwindi) have apparently served as a connective area between adjacent regions. This region is thus an important 'linkage' within the greater Lacustrine Rift, and likely provided a forest corridor of suitable habitat between now disconnected montane blocks. This area has been greatly impacted by human activity during the late Holocene (and now in the Athropocene), and is home to some of Africa's highest population densities [53, 76]. However, it is unclear how much species have been able to adapt to human activity within the region, and research should be performed on whether montane birds are capable of dispersing through Afromontane farming habitats [13].

Standing variation in populations can allow evolution to occur more quickly when selective pressures occur [17]. As the climate changes and populations are forced to adapt to novel climatic regimes and changing conditions, larger amounts of standing variation may allow for faster evolutionary responses and perhaps increase species' ability to persist. By incorporating niche models and phylogeographic models, we are able to show that, in spite of range reductions as species move upslope, no major regions of genetic variability will be lost for our study species in the near future as long at montane regions are not deforested.

Most remaining forest in the Lacustrine Rift is restricted to high elevations within established National Parks. Because the comparatively inaccessible nature of much of the region (due to remoteness and insecurity), the level of protection in these parks can vary, and some major forests (including Mt. Kabobo) were not protected until relatively recently [11, 272]. Every major geographic region analyzed here possesses a protected area, providing hope that the genetic diversity of these species will be maintained if protected areas remain operational. However, ancillary regions (including the Lendu and Marungu Plateaus) are not currently within protected areas and have been severely deforested [142–144], raising questions of whether distinct populations from these areas will persist in the even if suitable climates exists.

5.6 Conclusions

Using machine-learning and minimum volume ellipsoids to produce distribution models for our twelve study species through different time periods, we find empirical evidence that geographically isolated areas can possess different amounts of connectivity with adjacent mountain ranges. Most notable, we find that the Rwenzori Mountains are best considered part of the main Lacustrine Rift along with Bwindi, Kahuzi-Biega, Kibira-Nyungwe, and Itombwe, whereas Mt. Kabobo should be considered as a separate conservation region. Similarly, we find that not all species respond to these geographic breaks in the same way, and that patterns of diversification and timing of diversification events are not uniform across Afromontane bird species. The Lacustrine Rift has likely experienced multiple periods of connectivity and isolation that have served to build genetic diversity in the species as a whole, and we find evidence of gene flow between several montane regions in our study. We are cautiously optimistic for the future of these populations as we confirm previous studies' conclusions that these species will not only persist, but that gene flow between these areas in the recent past and may continue with proper conservation action.

5.7 Acknowledgments

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5.8 Data accessibility

Supplemental figures are available in and other supplemental material are available via `https://github.com/jacobccooper/dissertation_appendices`.

5.9 Ethics statement

This study is based upon specimens available for public research archived at private and public research institutions. All other analyses are based on data freely available online.

Table 5.1: Species sampling used in this study, with geographic coverage for each species and for each site noted. ‘X’ denotes a sample from that species/site combination was used in this study, whereas ‘0’ denotes the species occurs there but no genetic samples from that locality were included in this study, and blanks denote that the species is not known from that geographic area.

Species	**Rwenzori**	**Bwindi**	**Kibira-Nyungwe**	**Kahuzi-Biega**	**Itombwe**	**Kabobo**	**Site coverage**
Batis diops	**X**	**X**	**X**	**X**	**0**	**X**	**83.3%**
Sylvietta leucophrys	**X**	**X**	**X**	**X**	**X**	**X**	**100.0%**
Graueria vittata		**0**	**X**	**X**	**0**		**33.3%**
Oreolais ruwenzorii	**X**	**X**	**X**	**X**	**0**		**66.7%**
Iduna similis	**X**	**X**	**X**	**X**	**X**	**0**	**83.3%**
Phylloscopus laetus	**X**	**X**	**X**	**X**	**X**	**X**	**100.0%**
Sylvia atriceps	**X**	**X**	**X**	**X**	**X**	**0**	**83.3%**
Cossypha archeri	**X**	**X**	**X**	**X**	**0**	**X**	**83.3%**
Chamaetylas poliophrys	**X**	**X**	**X**	**X**	**0**	**X**	**83.3%**
Cyanomitra alinae	**X**	**X**	**X**	**X**	**X**	**X**	**100.0%**
Cinnyris regius	**X**	**X**	**X**	**X**	**0**	**X**	**83.3%**
Ploceus alienus	**X**	**X**	**X**	**X**	**0**		**66.7%**
Species Coverage	**91.7%**	**91.7%**	**100.0%**	**100.0%**	**41.6%**	**58.3%**	

Table 5.2: Sequences used to construct genetic relationships within this study.

Species	**ATP6**	**ND2**	**ND3**	**β-Fib5**	**TGF-β2**
Batis diops	**X**	**X**	**X**		
Sylvietta leucophrys	**X**	**X**	**X**		
Graueria vittata	**X**	**X**	**X**		
Oreolais ruwenzorii	**X**	**X**	**X**		
Iduna similis		**X**	**X**		
Phylloscopus laetus		**X**	**X**		
Sylvia atriceps	**X**	**X**	**X**		
Cossypha archeri	**X**	**X**	**X**		
Chamaetylas poliophrys		**X**			
Cyanomitra alinae	**X**	**X**			
Cinnyris regius	**X**	**X**		**X**	**X**
Ploceus alienus	**X**	**X**	**X**		
COVERAGE	**75.00%**	**100.00%**	**75.00%**	**8.33%**	**8.33%**

CHAPTER 6

MULTIPLE LINES OF EVIDENCE INDICATE ONGOING ALLOPATRIC AND PARAPATRIC DIVERSIFICATION IN AN AFROMONTANE SUNBIRD (*CINNYRIS REICHENOWI*)

6.1 Abstract

Africa's montane ecosystems are noteworthy not only for their isolation but for their morphologically similar bird populations that inhabit geographically disparate localities. Many species possess range disjunctions in excess of 2,000 km and appear to represent populations that have been isolated since at least the last Ice Age, including the Northern Double-collared Sunbird (*Cinnyris reichenowi*). Recent work on other Afromontane birds has demonstrated substantial phylogeographic structure can exist in phenotypically similar populations, with cryptic species occurring parapatrically within the same mountain range. We explored genetic, morphological, and ecological diversity within *C. reichenowi* to assess whether cryptic regional diversification occurs across the disjunct portions of this species' range. Within *C. reichenowi*, we find consistent patterns of morphological disparity that coincide with genetic diversification between xeric and wet montane populations within the Cameroon Line in the western population, and clear genetic differentiation between western and eastern populations. Our research demonstrates that the geographically isolated populations of *C. reichenowi* represent different species, and that ecological diversification is shaping populations within Central Africa. We show here that two named populations should be recognized as members of a western species (*C. preussi*) in the Northern Double-collared Sunbird complex: nominate *C. p. preussi* in the Cameroon Line montane forests, and *C. p. genderuensis* in the more xeric interior of Cameroon and the Central African Republic, likely occurring in adjacent Nigeria as well.

6.2 Introduction

Africa's montane ecosystems are dominated by multiple, large, isolated massifs that are mostly concentrated in the eastern part of the continent along the Rift Valleys [112]. These regions are home to a significant amount of the biodiversity inherent to the African continent (~14% of breeding bird species are endemic), and have potentially acted as a source of African bird diversity through time [45, 112, 113]. One of the most speciose groups in these montane regions is the sunbirds of the genus *Cinnyris* (Nectariniidae), a group of 53 nectarivores/insectivores that reach their maximal diversity in the Afrotropics [63]. One specific subgroup, the double-collared sunbirds, is primarily a montane radiation found throughout the Afrotropical highlands. Double-collared sunbirds comprise ~18 species and ~32 described taxa [63], although exact species limits within the group are still incompletely resolved. The vast majority of these taxa occur in eastern Africa, and they reach their maximal diversity within the Eastern Arc Mountains and the Albertine Rift Mountains of East Africa, where ~50% of the currently recognized species are endemic [63, 317] and speciation appears to have been facilitated by complex geography and turnover pulse dynamics [47, 113, 355]. Only one montane species of double-collared sunbird, the Northern Double-collared Sunbird (*Cinnyris reichenowi*), occurs in northwestern Sub-Saharan Africa, possessing a disjunct distribution between the Albertine highlands and the Cameroonian highlands (Figure 6.1) [43, 317]. The uniqueness of *C. reichenowi* is further illustrated by the species' apparently broad ecological niche breadth, occurring both in the highlands and in adjacent foothill regions of the Adamawa Plateau and smaller outlying highlands of Eastern Africa (*e.g.*, the Imatong Mountains of South Sudan and Uganda; Figure 6.2) [43, 71, 72, 317]. Multiple other pan-Afromontane taxa share this distribution pattern of disjunction between eastern and western montane regions (*e.g.*, Brown-capped Weaver *Ploceus insignis* and Oriole Finch *Linurgus olivaceus*), but few of these taxa occur in both the highlands and the adjacent lower elevations.

While data are limited, the complex phylogeographic relationships across equatorial

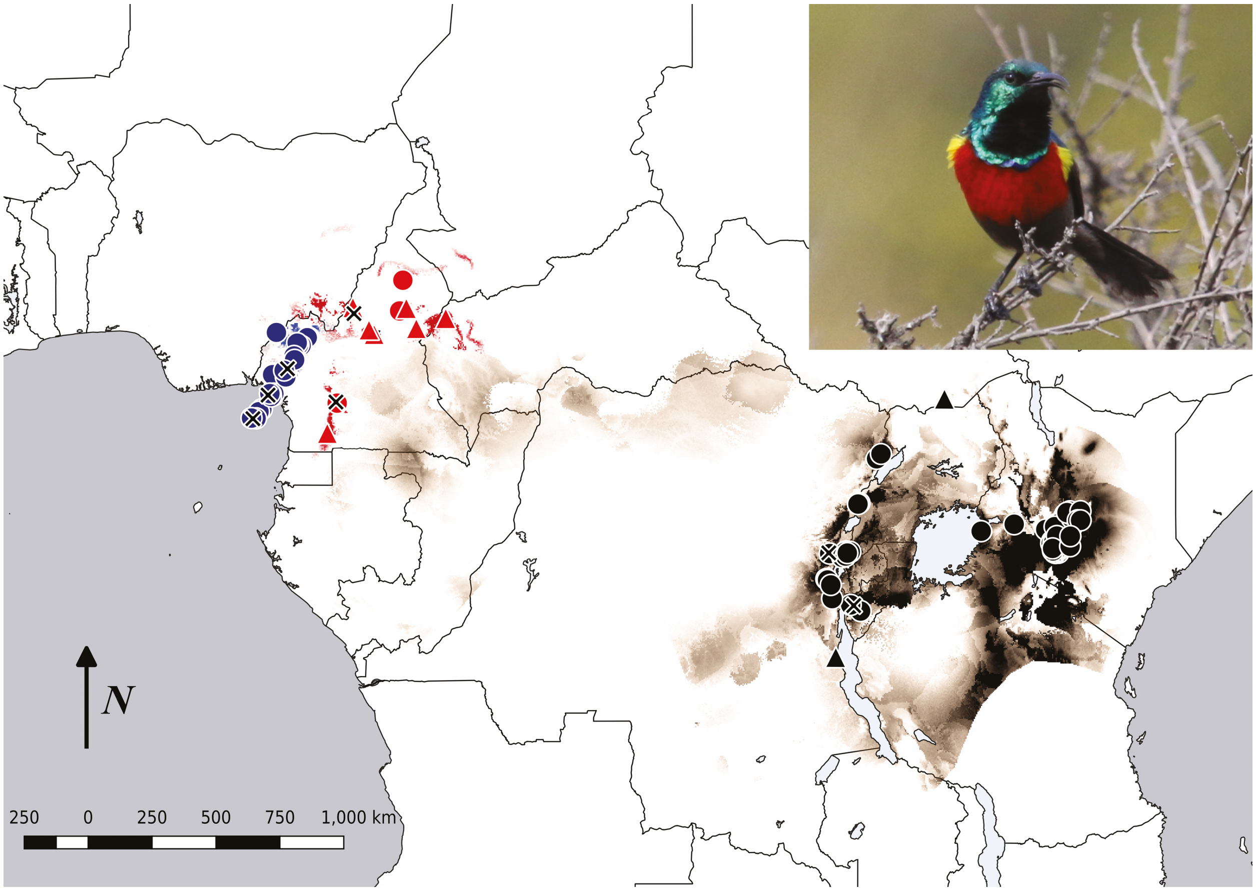

Figure 6.1: Most suitable areas for each population of *Cinnyris reichenowi* sensu lato based on ecological niche modeling using minimum volume ellipsoids. Populations are shown with their training point localities, with occurrence localities shown as circles and georeferenced specimen records shown as triangles. Sequenced localities are shown with a superimposed 'X'. Shaded areas represent a specified distance from the ellipse centroid, with Mahalanobis distances of 0–3 fully colored and Mahalanobis distances 3–5 fading to white. The hard line on the southern edge of the distribution represents the edge of the dispersal (**M**) polygon used for modeling; areas suitable for *C. reichenowi* in Tanzania are occupied by other species of *Cinnyris* not included in this study. Country names are provided in Figure 6.2. (Inset) *Cinnyris reichenowi preussi* from Bioko Island, Equatorial Guinea by Jacob C. Cooper, ML23308951.

Afromontane habitats suggests that climatic fluctuations (*i.e.* a turnover-pulse dynamic) may be driving diversification and evolution in these taxa, allowing for multiple colonization events leading to increased species diversity or increased genetic diversity within individual taxa [112, 275, 349, 355]. Recent research has shown a complicated pattern of trans-African colonization within other bird taxa, with the broadest sampled bird group being the montane sooty boubous *Laniarius fuelleborni* sensu lato [353]. *Laniarius fuelleborni* sensu lato are distributed across the Eastern Arc Mountains, the Albertine Rift Mountains, and the Cameroon Highlands, and consist of 4 reciprocally monophyletic groups including 2 that are elevational parapatric within the Albertine Rift highlands despite not being the others' closest relatives [30, 353]. *Laniarius* sooty boubous, similar to many pan-Afromontane bird groups, possess their maximal diversity in East Africa, with only one species (*Laniarius poensis*) reaching the Cameroonian highlands [63]. Limited genetic information exists for other groups, with the most extensive Afromontane studies being presented by Vaz da Silva (2015) [349]. These studies show widely varying patterns of genetic exchange and isolation across the Afromontane highlands, with several species having their Cameroonian Highland populations embedded within broader East and Southern African lineages (*e.g.*, Evergreen-forest Warbler *Bradypterus lopezi*, hill babblers *Sylvia abyssinica* superspecies, Bocage's Akalat *Sheppardia bocagei*, and Thick-billed Seedeater *Crithagra burtoni*) [349]. Although Vaz da Silva's (2015) [349] study was specifically focused on taxa that also occur in Angola, it illustrates the complicated nature of Afromontane relationships, and demonstrates that multiple migration events may have occurred between East and West Africa (*e.g.*, for the *Sylvia abyssinica* superspecies).

Within *C. reichenowi*, intermediary foothill populations suggest a larger climatic envelope exists within the ecological niche of *C. reichenowi* than for other pan-Afromontane species [174]. Thus, the species may be more likely to have eastern and western populations come into contact and exchange genes during these climactic cycles [350]. The taxonomic history of this species, however, indicates that local diversification may be occurring, even if the patterns are not clear. At present, there are only two recognized subspecies within *C. reichenowi*, the eastern nominate *reichenowi* [311] and the western *preussi* [292], with two other described subspecies considered conspecific with *preussi* [63]: *genderuensis* from xeric interior Cameroon [293], and *parvirostris* from Bioko Island [98]. A fifth taxon, *kikuyuensis*, was originally described based on one specimen from Kenya [240], but this population falls within the range of variation of other populations of *reichenowi* [120]. These subspecies have been primarily described based on subtle (and sometimes inconsistent) phenotypic and morphological differences, and overlap in characters without consistently discernible geographic variation has led to confusion on subspecific distributions [15, 20, 98, 136]. We hypothesize that the synonymized taxon *genderuensis* is reflective of the ongoing diversification of western populations of *C. reichenowi*, and that this diversification led to taxonomic uncertainty in the region. To clarify patterns of diversification and test taxonomic treatments within *C. reichenowi* in light of described phenotypic, morphologic, and ecologic variation within the species, we gathered molecular, morphometric, and ecological data with a specific focus on western populations to understand their connectivity and evolutionary history. Specifically, we sought to determine whether there are consistent morphological differences across *C. reichenowi* populations, how many colonization events occurred to form the West African population(s), and whether there is ongoing (or recent) connectivity between *C. reichenowi* populations given their presumably broad ecological niche.

6.3 Methods

6.3.1 Sampling and DNA extraction

For genetic data, we sampled 24 individuals, with a focus on western *C. reichenowi* (14 individuals, Table 1). We chose *Cinnyris regius* as an outgroup as it is regionally sympatric with nominate *C. reichenowi*. All individuals are vouchered museum specimens. We selected *C. reichenowi* samples from across its distribution, with 4 samples from the Eastern portion

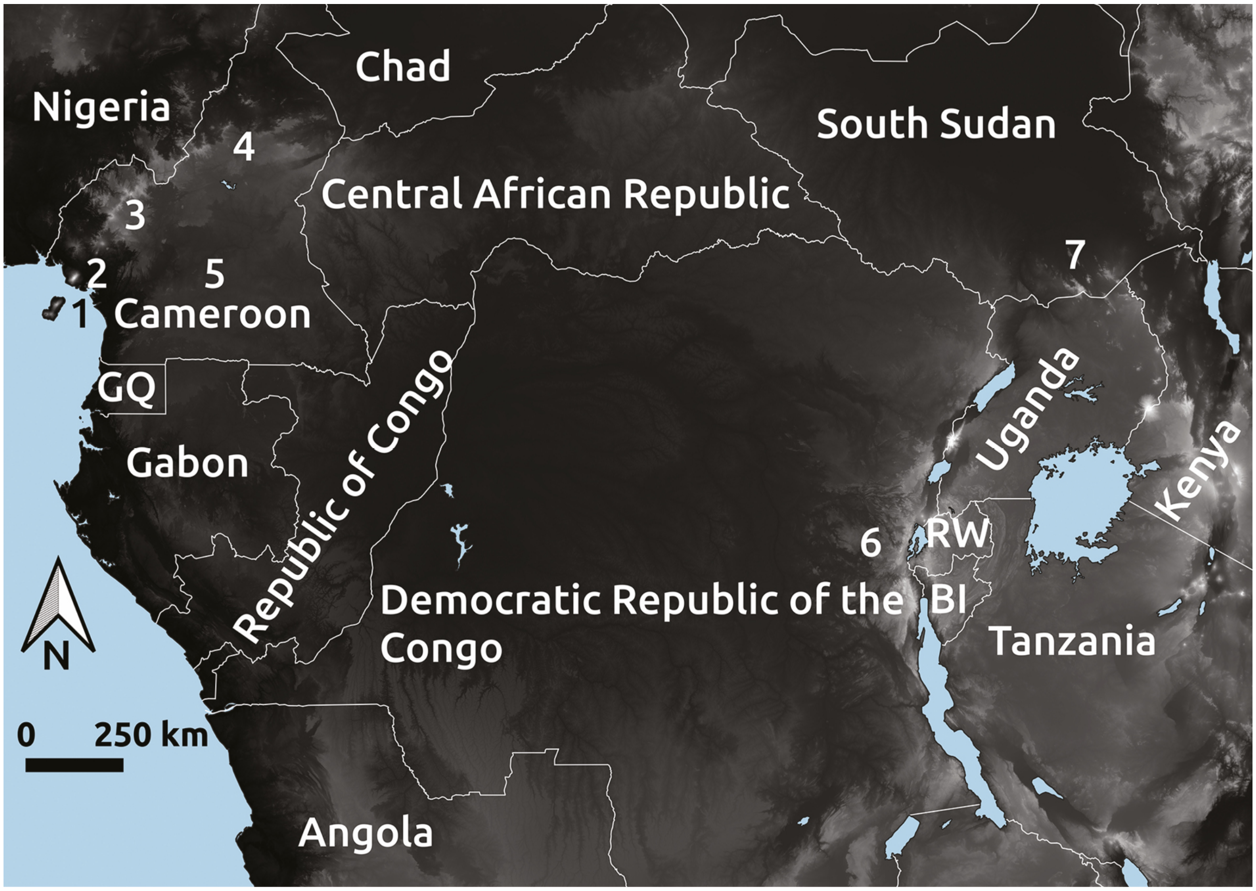

Figure 6.2: Map of Central and Eastern Africa, showing countries referenced in this study and the locations of the following montane localities: (1) Bioko Island, Equatorial Guinea; (2) Mt. Cameroon, Cameroon; (3) Bamenda Highlands, Cameroon, and Nigeria; (4) Adamawa Plateau, Cameroon, Central African Republic and Nigeria; (5) highlands near Yaoundé, Cameroon; (6) Kahuzi-Biega Highlands, Democratic Republic of the Congo; (7) Imatong Mountains, South Sudan, and Uganda. The following country abbreviations are used: BI = Burundi, GQ = Equatorial Guinea, RW = Rwanda.

of the range (Kahuzi-Biega, the Democratic Republic of the Congo and Kibira, Burundi), 3 samples from interior Cameroon (Babadjou, Genderu, and Yaoundé), 4 samples from Mt. Cameroon, Cameroon, and 3 samples from Bioko Island, Equatorial Guinea (Figure 2). We obtained 10 *C. regius* samples from throughout their range in the Albertine Rift, overlapping wholly with the distribution of *C. reichenowi* samples from the same area (Table 1). When available, we obtained frozen tissue samples for all populations, but we used toepad samples for 7 historical samples of *C. reichenowi* representing important geographic regions for western populations (Table 1). We extracted tissues from all samples using the Qiagen DNeasy Blood and Tissue extraction kit. We assessed the quality of DNA extractions using agarose gel electrophoresis for frozen tissue samples only, and quantified the DNA concentration of all samples using a Qubit fluorometer (Fisher Scientific Equipment) before continuing to perform our library preparation for next-generation sequencing.

6.3.2 Next-generation sequencing

We used sequence capture of ultraconserved elements (UCEs) for all of our samples as this method has proven successful for incorporating toepads into datasets with modern tissue samples [25, 236]. We followed the library preparation protocols put forth by Faircloth et al. (2012; ultraconserved.org) [107]. This method relies on the use of 180-base pair (bp) synthetic baits to capture genomic sequences that are widely orthologous across tetrapods [107]. Core UCE regions are largely conserved across species (and even families), but the flanking regions possess significantly more variation that makes UCEs useful for analyzing relationships at deep and shallow timescales [153, 231, 235, 321, 379]. After performing the aforementioned library preparation steps, we sent our samples to the Genomics and Cell Characterization Core Facility at the University of Oregon, USA where they were sequenced on an Illumina HiSeq 4000. We processed all raw data in tandem. Raw data reads are available via GENBANK (see data availability statement).

6.3.3 UCE processing

We processed raw data through the PHYLUCE pipeline [106], which allows for multiple steps of quality control followed by aligning and assembling the UCE loci for subsequent analyses. We performed this pipeline as recommend by Faircloth (2016) [106], using Illumiprocessor [105] and Trimmomatic [42] to remove adapter contamination and low-quality base reads. We assembled reads into contigs using Trinity [139] with the default settings. We reviewed summary statistics of the data and proceeded to align data with 80% coverage between all samples (for full codes see Cooper et al. 2021; doi:10.5061/dryad.34tmpg4j0) [71].

We prepared the aligned data for analysis in RaxML [330] using the PHYLUCE interface. Using the provided commands for cleaning and concatenating data (phyluce.readthedocs.io), we took our samples of interest and aligned them using **mafft** v7.130b [195] and subsequently trimmed them using **GBLOCKS** 0.91b [335, 336]. Our alignment summary showed that we recovered 4,946 loci, with coverage decreasing rapidly after the 80% threshold (3,237 loci). Given this information, we opted to use the 80% coverage matrix for our primary analyses, though we also performed RaxML analyses with the 50% and 95% coverage matrices to compare topologies. Analyses were run using a bootstrapped approach through RaxML v8.2.4 [330]. We used the GTRGAMMA rate heterogeneity model with a non-partitioned dataset (similar to other studies using UCE data), set our random seed to 19,877, and set our bootstrapping random seed to 7,175 [379].

6.3.4 Single nucleotide polymorphisms

We followed the methods outlined by Zarza et al. (2016) [379] and used our individual with the highest sequence coverage, KU 132209 from Bioko, as our reference genome for aligning our other samples using the **BWA-MEM** algorithm [212]. We then followed the Zarza et al. (2016) [379] pipeline to sort reads in **SAMTOOLS** [213] before removing PCR duplicates in **Picard** (`https://broadinstitute.github.io/picard/`) and finishing the processing of the identified single nucleotide polymorphisms (SNPs) in **GATK** version 3.4.46 (Broad

Institute). We obtained our final SNP files via **VCFTOOLS** 0.1.15 (Danecek et al. 2011) where we parsed our SNP matrices for missing data and created two matrices that had minimum inter-SNP distances of 900 bp and 170 bp. We chose 900 bp to find dissociated SNPs, but we also kept the 170 bp matrix as this is the value at which the number of SNPs being removed at each iteration plateaus and we wanted to compare the performance of these two datasets when creating species trees. We used our resulting SNP matrices to create species trees in **SNAPP** [51] implemented via **BEAST** 2.5.0 [44]. We used the default settings and calculated parameters provided by the built-in formatter *BEAUTI* for a **SNAPP** run, and we ran the tree for 2 million generations sampling every 1,000 steps. We visualized the results in the **BEAST** application *DENSITREE* to assess the "fuzziness" (*i.e.*, potential gene flow and connectivity) of different populations.

We used principal component analyses (PCAs) to visualize the SNP variation in the samples. Due to similar topologies between datasets in **SNAPP**, we performed this step on the 170 bp SNP data. We analyzed SNP data in **R** 3.4.4 [285] using the package *LEA* [119] and visualized the data using the package *ggplot2* [369]. To determine if the observed groups were statistically differentiable, we performed discriminant function analyses (DFAs) on the same SNP data within **R** 3.4.4 [285]. These discriminant function analyses were conducted using the function 'lda' in the **R** package *MASS* [351], and they focused on separating *Cinnyris reichenowi reichenowi* from *Cinnyris reichenowi preussi*, and then further focused on genetic structure within *C. r. preussi*.

6.3.5 Mitochondrial data

We concatenated mitochondrial genomes to perform rough age estimations of diversification events. Using the raw reads and **Geneious** 9.1.8 [127], we were able to obtain and align near-complete mitochondrial genes for samples derived from fresh tissue samples. Using the built in **Geneious** proprietary software and the *MUSCLE* plug-in, we aligned the mitochondrial reads from our samples and created consensus sequences for each geographic region. Sites that had no support (or limited support for "any base" from only one or two individuals) were manually removed. We then trimmed all mtDNA sequences to be the same length and used **Geneious** to calculate similarity matrices between populations. We timed divergences using a calibration of 2% divergence per million years [122, 364].

6.3.6 Introgression tests

We used ABBA/BABA tests to look for evidence of past hybridization and introgression [95, 141, 372]. These tests analyze SNPs to determine if the sorting of mutations in more recently derived populations are close to random (as would be expected in a purely stochastic speciation event). Thus, in a tree with a topology of (((S1, S2) S3) Outgroup), there should be equal numbers of (((A, B) B) A) and (((B, A) B) A) patterns. Gene flow between the non-sister groups of S2 and S3 can lead to an excess of ABBA patterns (as long as S1 and S3 are not also hybridizing). We performed these ABBA/BABA tests using the 'doAbbababa' command in the program **ANGSD** [206]. Significant introgression events can be detected using Patterson's D-statistic [95, 141], and this method has been successfully used for UCEs harvested from birds [372, 379]. In order to analyze the significance of D statistics, we randomly resampled the entire SNP distribution to create a D distribution from which we could ascertain whether differences between populations are significantly utilizing a script made available in the program **ANGSD** [206, 379]. Z-scores resulting from these D-distributions were found by using **R** to calculate $2\times[1{-}pnorm(z)]$ [285], thus reflecting significant introgression when P is <0.025 or >0.975. These tests were primarily used in the comparative sense to understand relative amounts of gene flow between different populations.

Populations were further assessed using the 'snmf' function of the **R** package *LEA* [119]. This function estimates proportions of ancestry for individuals based on SNP data by means of non-negative matrix factorization (SNMF) and allows for testing different numbers of ancestral populations (k). In order to understand better the population structure within

C. reichenowi, we ran the analyses with this species only. We tested hypotheses of 1 to 6 ancestral populations (k), and used α parameters of 1, 50, 100, and 500 to compare the effects of this metric on the data.

6.3.7 Morphology

JCC visited 10 different museum collections and collected morphological data on *C. reichenowi* specimens [72]. Measurements were obtained by hand with Mitutoyo IP67 calipers and a standard wing ruler (AFO Banding Supplies, Manomet, Massachusetts, USA). Measurements were obtained of birds' wing chord (right-wing whenever possible), tail length, culmen length (from the base of the feather on the culmen to the tip as a straight line), bill depth (thickness at the base of the feathers on the mandible), bill width (at the base of the feathers on the maxilla), and tarsus (left tarsus when possible). Wing and tarsus selection were arbitrary and based on the handedness of JCC; if the chosen wing or tarsus was in poor condition or unavailable for measurement, the other wing or tarsus was measured. Data were visualized using individual boxplots by variable (executed in *R*), PCAs of the morphological variables using the 'rda' function of the package *vegan* in **R** [252], and Wilcoxon rank-sum tests to determine if populations differed with respect to individual measurements. We opted for Wilcoxon rank-sum tests as these tests are robust to different population sizes and potential non-normality [84]. As above, we performed discriminant function analyses using the *MASS* package function 'lda' [351], including a secondary run with *C. r. preussi* randomly subsampled 1,000 times at a sample size equal to that of *C. r. genderuensis* to account for unequal group sizes.

6.3.8 Ecological niche modeling

Occurrence data from eBird [96, 334] were downloaded in late 2018 (version relAug_2018) and combined with georeferenced specimen data (georeferencing performed by JCC via internet searches of localities, with verification of one specimen locality provided by S. Frahnert and P. Eckhoff, Museum für Naturkunde). Datasets for the eBird database and the georeferenced specimen database were combined and rarefied to 3 km using a custom script from J. D. Manthey (Texas Tech University), resulting in 98 points for *C. r. reichenowi*, 10 points for *C. r. genderuensis*, and 27 points for *C. r. preussi* [71, 72]. Environmental data were downloaded from the *ENVIREM* dataset [339]. *ENVIREM* data at each specimen locality were analyzed using the same analyses as morphological data to determine if there were any differences between the populations; namely, we performed PCAs, discriminant function analyses, and Wilcoxon rank-sum tests on environmental value extractions from the 30 arcsecond resolution dataset (1 km resolution at the equator). Extractions were performed in **R** using the package *raster* [157], and ecological niche models were only created using *ENVIREM* layers that had <85% correlation with the data layers that explained most of the PCA variation.

We used the *ENVIREM* 2.5 arcminute data (~5 km resolution at the equator) to create and train ecological niche models created using a custom script that ascribes minimum volume ellipsoids to the multivariate data. We used 2.5 arcminute data due to the processing requirements for the substantially larger 30 arcsecond dataset. The least correlated data layers for the PCA's (after removing those with high covariation) were: Thornthwaite aridity index, continentality, Emberger's pluviothermic quotient, maximum temperature of the coldest quarter, minimum temperature of the warmest quarter, precipitation of the driest quarter, and precipitation of the wettest quarter.

We opted for the use of minimum volume ellipsoids as they are easy to manipulate for varying sample sizes (as long as the number of data points exceeds the number of environmental layers used) [247, 347, 351], they rely on presence data only with no pseudoabsences, and they obtain similar results to more intensive methods such as *MAXENT* when data bias is present [176, 271]. The distribution of one population (*genderuensis*) is also incompletely known, and we wanted to avoid any distribution gap issues that may arise from drawing pseudoabsences within *MAXENT*. This script was executed in **R** 3.4.4 [285], and based on code obtained from Jorge Soberón at the University of Kansas [71]. We took custom biogeographic envelopes for each population created in QGIS 2.8 [281] and used the **R** packages *maptools* [38] and *raster* [157] to restrict the environments for each species [73, 255, 325]. These biogeographic regions were drawn by hand and encapsulate the region in which the species is found while being bounded as much as possible by known biographic barriers (*e.g.*, the Congo River). Biogeographic areas used here are available in the Online Supplemental Material, and this method is elaborated further in Cooper and Soberón (2018) [73]. Ellipsoids were fit to the data using Mahalanobis distances [226] implemented in **R** via the packages *ellipse* [247] and *MASS* [351].

We projected the distance of each cell to the centroid of the species' niche to determine suitability across the African continent. These projections were also performed to the past datasets of the Holocene (6,000 years ago) and Last Glacial Maximum (22,000 years ago) provided within *ENVIREM* [339], with models averaged across the predictions for all three global circulation models available. Projections were created for gross distance to the centroid, with some maps converted to "thresholded distance" depicting how many standard deviations each cell was located from the average distance from centroid of the actual occurrence points. For these thresholded rasters, everything less than or equal to the average distance was given a value of 'one', and everything within one standard deviation further was assigned a '2', etc. These averaged maps were subsequently combined to understand which regions were historically most similar to the modern climactic envelope for all populations of *C. reichenowi*, and where likely avenues of colonization were located.

6.3.9 Ecological niche divergence

We tested ecological divergence by comparing our actual models of suitability to "null" models created from random points drawn from within each species' aforementioned accessible area [135, 237, 358]. Random points were created within the accesible areas using the 'spsample' function in *sp* [41, 262] and *maptools* [38] in **R** [285], and subsequently used to train null niche models using the aforementioned ellipsoidal methodology. We repeated this step 100 times to create a random null distribution for ecological niche models derived from each accessible area. Using the function 'nicheOverlap' in *dismo* [163], we obtained Schoener's D values for (1) the true comparison of the models for each species, (2) the comparisons of population A to the random models of population B, and (3) the comparisons of population B to the random models of population A. Schoener's D is a statistic designed to look at similarity, with a value of one being identical and a value of zero being wholly different. This was performed pairwise for every combination of *C. r. reichenowi*, *C. r. preussi*, and *C. r. genderuensis*, both with the entire point dataset and repeated for the 80% of points that are closest to the niche centroid (similar to the thresholds created for distributions). We obtained Z scores and converted them to P values for these combinations to determine if the true comparison was greater than the random distributions (*i.e.*, that niche divergence has occurred) or if it was less than the random distribution (*i.e.*, that niche conservatism is occurring). While niche divergence is significant from an evolutionary perspective, niche conservatism is often viewed as the "expectation" or null model of niche divergence tests between closely related species given their shared evolutionary histories and their often parapatric or allopatric distributions [267, 269].

6.4 Results

We obtained a minimum read count of 509,662 (toepad sample of FMNH 273746 *C. r. preussi* collected in 1937) and a maximum read count of 4,743,968 (KU 132209 *C. r. preussi*, tissue sample from 2016; Table 1). The average read count for tissues was 2,942,188, whereas for toepads the average was 2,790,815. In all analyses, we found high support for three nested monophyletic groups: *C. regius*, *C. r. reichenowi* (East Africa), and a western clade of *C. r. genderuensis* and *C. r. preussi* (Figure 6.3). Trees largely agreed in the topology of major nodes, with the exception of the location of the long-branched FMNH 122395 (*C. r. genderuensis*). Broader genetic matrices (80% shared between all individuals and below) recovered high support of FMNH 122395 being sister to the other *C. r. genderuensis* sample, FMNH 189462, and of *C. r. genderuensis* being a monophyletic group sister to *C. r. preussi*. However, matrices with more alignments shared across individuals (and, therefore, fewer sequences for analyses, such as the 90% and 95% coverage matrices) recovered *C. r. genderuensis* as polyphyletic, with FMNH 122395 sister to other *C. r. preussi* with an outgroup of FMNH 189462. In all iterations, the branch leading to FMNH 122395 is significantly longer than the branch length of any other sample. We believe this long branch length is the result of missing data within the sample rather than contamination due to the consistent placement of this taxon with its assumed sister individual based on geography and morphology [166, 236]. We also ran separate iterations of tests without FMNH 122395, which did not significantly alter the results presented herein. Given that larger amounts of data and SNP matrices recover FMNH 122395 as a member of the *C. r. genderuensis* clade, we present here our results for the 80% coverage matrix. Within *C. r. preussi*, there is limited but consistent geographic structure, with Bioko Island birds existing as a separate cluster from Mt. Cameroon samples, and these coastal populations are sister to the interior sample from the Bamenda Highlands. RaxML analyses of the dataset find strong support for *C. r. genderuensis* as sister to *C. r. preussi*, but low support for the node relating the two *C. r. genderuensis* to each other.

6.4.1 Species trees

RaxML analyses recovered 100% bootstrap support for the clades of *C. regius*, *C. r. reichenowi*, a monophyletic group of all western individuals, and a monophyletic group of *C. r. preussi* (Figure 6.4). The *SNAPP* tree showed limited separation between mountain ranges in East Africa for both *C. regius* and *C. r. reichenowi*, and recovered structure between the mountains of Cameroon, with each major western massif being recovered as a unique population (Figure 6.3). The SNAPP analysis identified *C. r. genderuensis* as a monophyletic group with 99% posterior support. Given these strong partitions, we treated

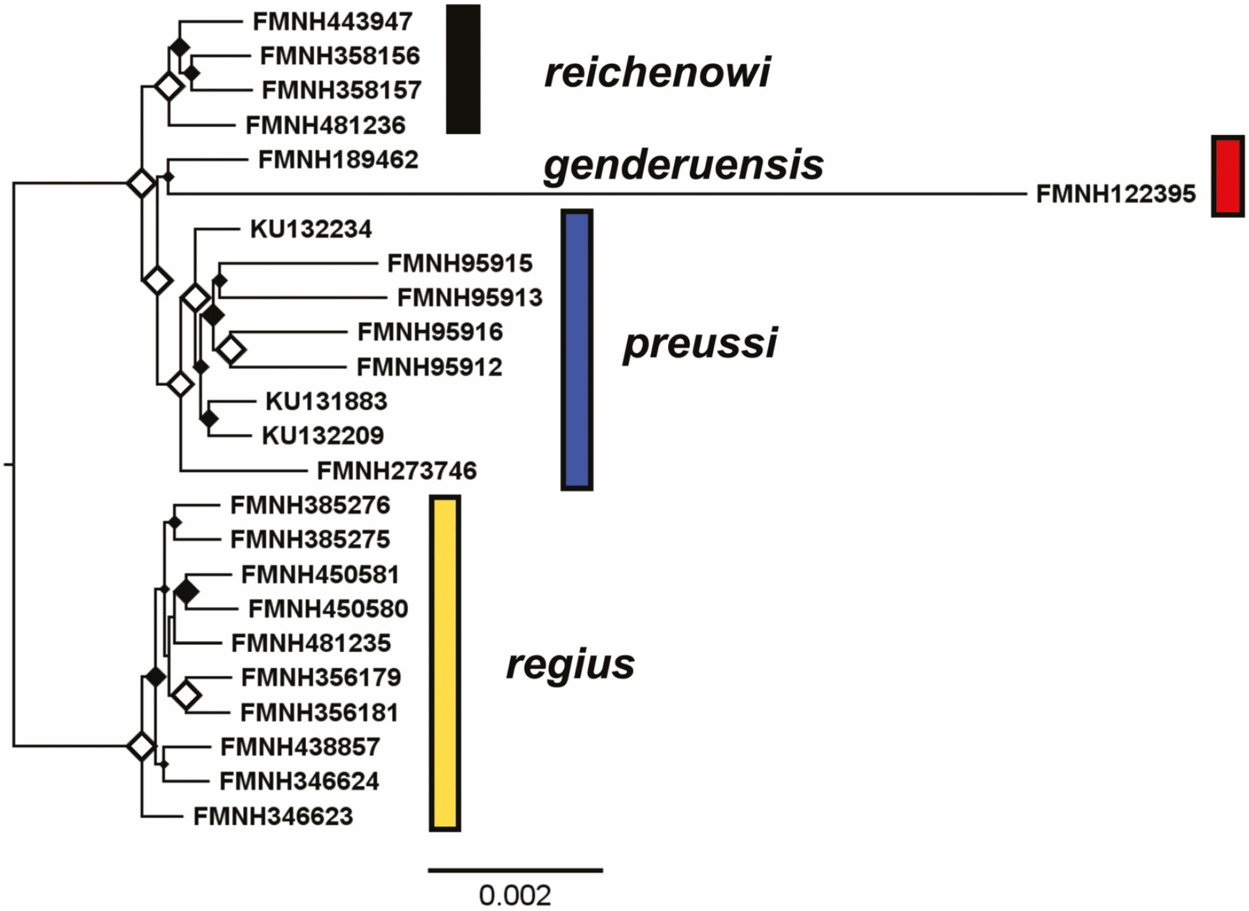

Figure 6.3: RaxML constructed a phylogeny of relationships within *Cinnyris* sunbirds sampled herein using UCE data. Note that FMNH 122395 (*C. r. genderuensis*) possesses a long branch, but is consistently recovered as being a well-supported part of the same clade as FMNH 189462 in all analyses. Internal nodes are sized relative to support, and nodes with white centers have 90% support.

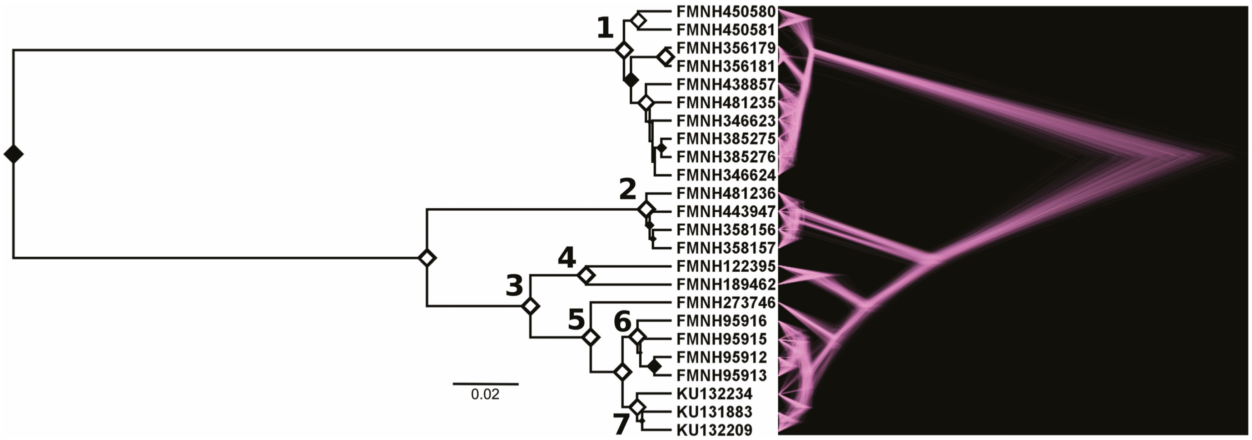

Figure 6.4: **SNAPP** phylogeny of *Cinnyris* sunbirds used in this study with node size reflecting support (left) and the raw **SNAPP** output showing the aggregated species trees created during the analyses, where the bolder lines indicate stronger consensus for the relationship (right). Nodes with white centers have 90% posterior probability support. Nodes are numbered as follows: (1) *C. regius regius*; (2) *C. reichenowi reichenowi*; (3) western *C. reichenowi*; (4) *C. r. genderuensis*; (5) *C. r. preussi*, with FMNH 273746 as the only *preussi* individual from the interior highlands of Cameroon near Babadjou, Ouest [136]; (6) *C. r. preussi* from Mt. Cameroon, Cameroon; and (7) *C. r. parvirostris*, the Bioko population of *C. r. preussi* once considered a separate subspecies.

C. r. reichenowi, *C. r. genderuensis* and *C. r. preussi* as separate entities for other analyses. Using mitochondrial genes, we obtain a divergence time of 0.87 mya for eastern vs. western populations of *C. reichenowi* and 3.85 mya for the divergence between *C. regius* and the *C. reichenowi* group (Table 2).

6.4.2 Introgression and connectivity

Our PCA analyses of genotypes confirmed that there were 4 clusters from the overall dataset, corresponding to *C. regius* and each of the 3 *C. reichenowi* populations. When analyzing only *C. reichenowi*, we recovered strong separation between eastern and western populations along the first principal component axis (19.3% of variance explained) and separation between *C. r. genderuensis* and *C. r. preussi* along the second principal component axis (10.7% of variance explained; Figure 6.5). In this analysis, Mt. Cameroon and Bioko populations clustered together, while our interior sample of *C. r. preussi* from the Bamenda

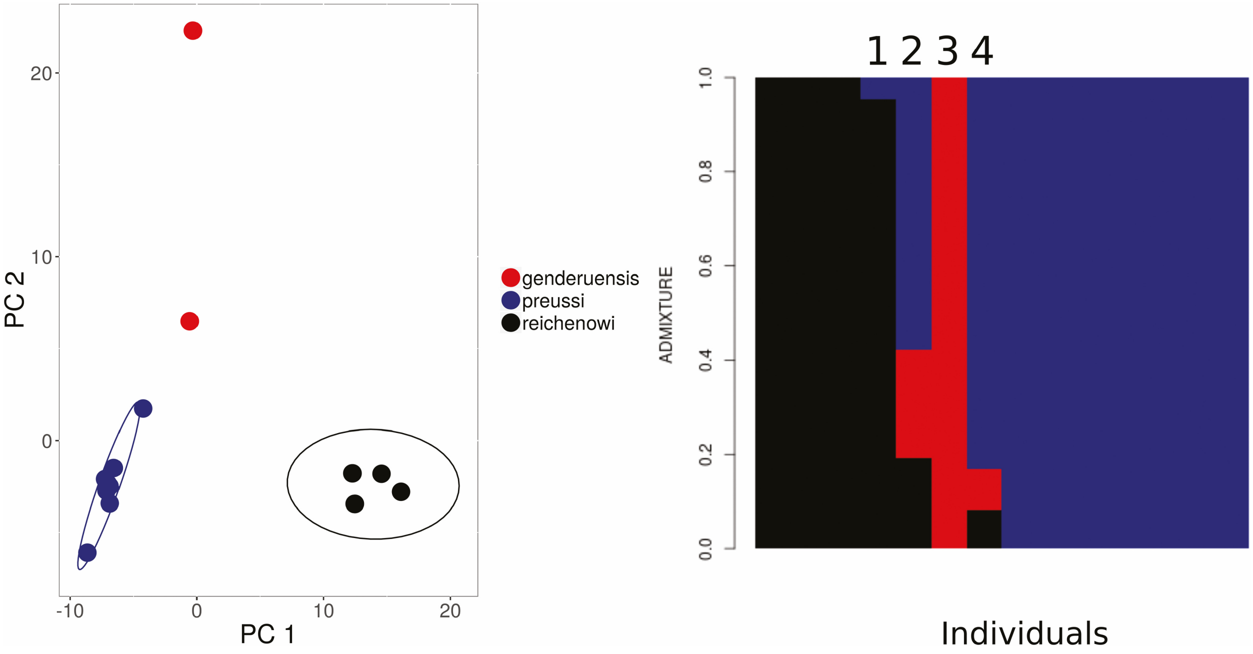

Figure 6.5: Principal component analysis plot of single nucleotide polymorphism (SNP) variation in *Cinnyris reichenowi* (left) and SNMF admixture plot of 14 individuals (right) ordered from NE to SW (*i.e.*, from Kibira NP, Burundi to Bioko, Equatorial Guinea). The four individuals exhibiting admixture are (1) FMNH 481236 *C. r. reichenowi*, Kahuzi-Biega, DRC; (2) FMNH 122395 *C. r. genderuensis*, Genderu, Cameroon; (3) FMNH 189462 *C. r. genderuensis*, Yaoundé, Cameroon; and (4) FMNH 273746 *C. r. preussi*, Babadjou, Cameroon.

Highlands was located between the coastal cluster and the *C. r. genderuensis* points, but still closer to coastal *C. r. preussi* (Figure 6.5). Subsequent principal components began separating individuals within each subspecies, with the third principal component (8.82% variance explained) predominantly separating individuals from the Eastern portion of the range (*C. r. reichenowi*) from each other. The problematic *C. r. genderuensis* sample came out as an isolated point, but was still most associated with the other *C. r. genderuensis* sample in these analyses.

The discriminant function analyses performed on the principal components of the SNP data were performed iteratively on different groupings of individuals to test subspecific assignments. We limited these tests to the major genetic groupings recovered from previous analyses. Our test of separating all three major genetic groups (*C. r. reichenowi*, *C. r. genderuensis*, and *C. r. preussi*) had a success rate of 92.9% (n = 14), only confusing one *C.*

r. genderuensis individual with *C. r. preussi*. The DFA was 100% successful in separating the broader groups of *C. r. reichenowi* and *C. r. preussi* (including *genderuensis*).

The ABBA/BABA tests of gene flow were similarly performed in an iterative fashion with multiple populations and with different levels of outgroup to better understand the gene flow dynamics. We used a hierarchical approach towards declaring outgroups, comparing gene flow levels against outgroups of *C. r. regius*, *C. r. reichenowi*, and *C. r. genderuensis* as we moved towards the most closely related populations (Bioko Island and Mt. Cameroon *C. r. preussi*; Table 3). Evidence of connectivity between all groups was evident when we performed the test with *C. regius* as an outgroup (largest $P = 0.002$), with the most significant P values being found for randomized scenarios that placed the western groups (*C. r. genderuensis* and *C. r. preussi*) as sister to each other. Within western taxa, gene flow was again recovered for every scenario, with the highest levels of gene flow ($P < 0.001$) being recovered between subpopulations of *C. r. preussi* on the coast and in the adjacent interior. When *C. r. genderuensis* was used as an outgroup and *C. r. preussi* was divided into interior (*i.e.*, Bamenda Plateau) *C. r. preussi*, coastal (*i.e.*, Mt. Cameroon) *C. r. preussi*, and Bioko *C. r. parvirostris*, significant levels of gene flow were only found between coastal and Bioko populations ($P < 0.001$), with the individual from the interior *C. r. preussi* having non-significant levels of gene flow with coastal birds ($P = 0.41$).

Determining population composition using ‘snmf’ indicated that the most likely scenario involved two ancestral populations split between east and west within *C. reichenowi*. The second most likely scenario was three ancestral populations. Visualizing three population divisions at $\alpha = 100$ showed that *C. r. reichenowi* and coastal *C. r. preussi* are separate groups, but the status of *C. r. genderuensis* is not fully resolved (Figure 6.5). One individual of *C. r. reichenowi* from Kahuzi-Biega, DRC, shows some admixture with western *C. r. preussi* populations(5%). One individual of *C. r. genderuensis* (FMNH 189462) from Yaoundé was recovered as its own group; however, the other *C. r. genderuensis* individual demonstrated 60% admixture with *C. r. preussi* and 20% admixture with *C. r. reichenowi*.

Similarly, the interior *C. r. preussi* individual from Babadjou, Cameroon showed 10% admixture with both *C. r. genderuensis* and *C. r. reichenowi*.

6.4.3 Morphological data

After data cleaning, we retained 20 individuals of *Cinnyris regius* and 383 individuals of *C. reichenowi* for analyses (Table 5). We analyzed sexes independently. Analyses of *C. regius* were limited to males, as these constituted 17 of the 20 samples in our dataset. All individuals of *C. regius* were from the nominate population and included localities used for genetic sampling. Our *C. reichenowi* sample contained 263 males and 120 females. For all sunbirds, PC1 captured a large proportion of the variation associated with all variables, with the most important contributions being culmen length and bill width, with large-billed birds having more negative PC1 values. PC2 captured more of the variation for bill depth and tarsus length.

Within both the male and female datasets, *C. r. preussi* individuals largely overlapped in morphological space with *C. r. parvirostris* (Tables 4 and 5). These western populations exhibited limited overlap with *C. r. reichenowi* individuals from the East. *C. r. genderuensis* overlapped in morphometric space predominately with *C. r. reichenowi*, with only a few individuals from the male and female populations being morphologically inseparable from other western populations (Figure 6.6). These populations are morphologically similar, but do differ with respect to right-wing chord and culmen length (Tables 4 and 5). Specimens of *C. r. genderuensis* that are morphologically similar to *C. r. preussi* are from the interior xeric plateaus of Cameroon where *C. r. preussi* is presumed absent; the most morphologically '*preussi*' individual assigned as genderuensis came from Tello, Adamawa, Cameroon (RMCA 75-3-A-438).

Within the male dataset, there were three individuals whose subspecific identity was marked as "unknown" due to their localities' ambiguity or presence in the presumed *genderuensis-preussi* contact zone in the middle elevations of the western Bamenda Plateau; all 3 of these

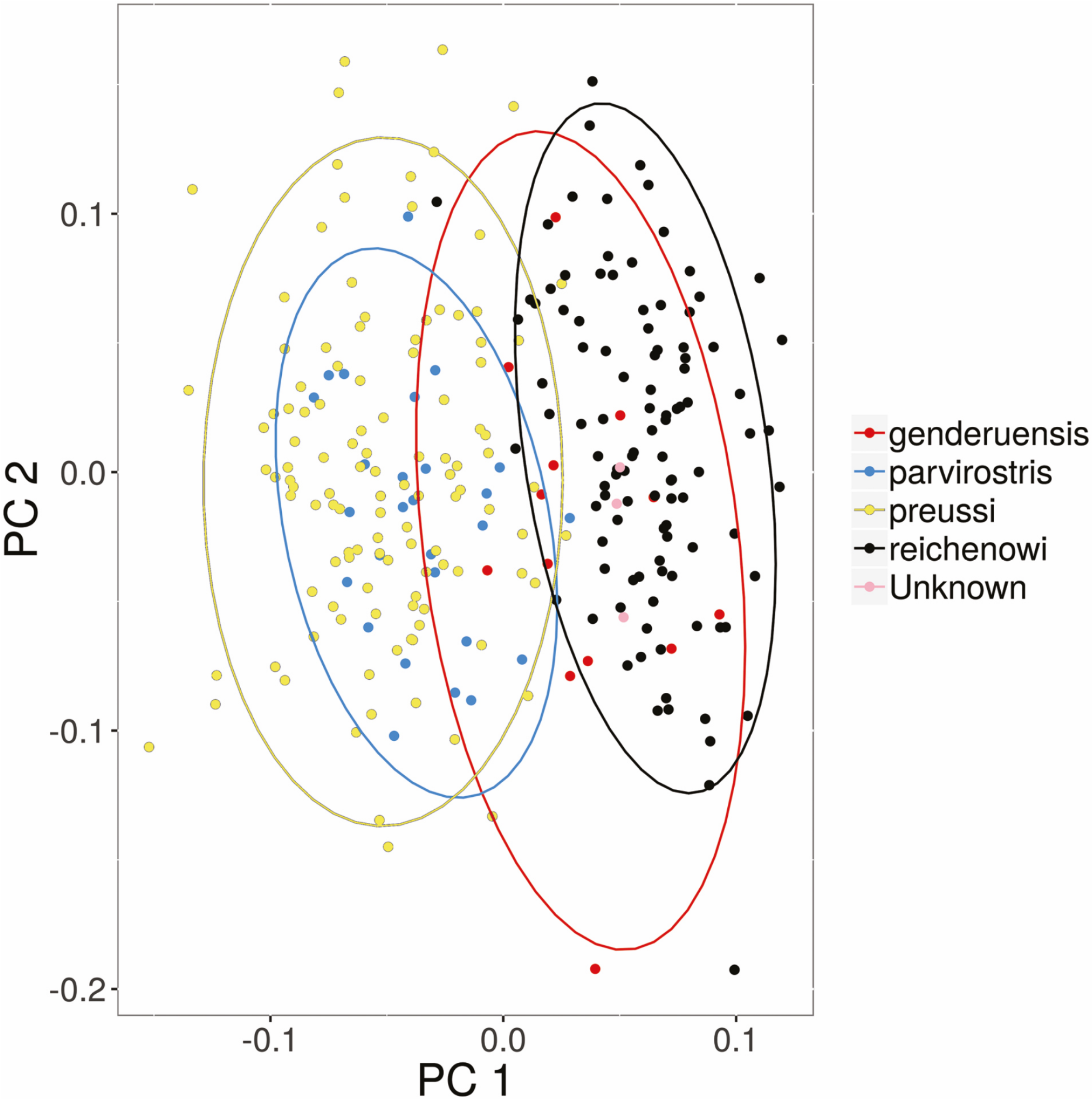

Figure 6.6: Principal component analysis plot of morphological variation within male *Cinnyris reichenowi*. Note that almost all *C. r. genderuensis* fall within the range of variation of *C. r. reichenowi*; those that fall within the range of variation of *C. r. preussi* are from near Tello on the Adamawa Plateau (Royal Museum for Central Africa) and were identified as *genderuensis* by range. *C. r. parvirostris* refers to birds from Bioko Island, which we found indistinguishable from mainland *C. r. preussi* contra Eisentraut (1965) [98].

individuals were within the range of variation expected for *genderuensis* and not *preussi* (MNMH 2005.995 from an unspecified locality, ZMB 2000.7987 from an unspecified locality, and ZMB 75.79 from the Bangwa Highlands, Cameroon). A closer inspection of *C. r. preussi* (excluding *parvirostris*) and *C. r. genderuensis* in the male subset revealed that these populations differ significantly with respect to wing chord (Wilcoxon rank sum test, $W = 187.5$, $P < 0.001$, *preussi* being 4.79% larger than *genderuensis*), tail length (Wilcoxon rank sum test, $W = 349$, $P = 0.001$, *preussi* being 6.01% larger than *genderuensis*), culmen length (Wilcoxon rank sum text, $W = 57.5$, $P < 0.001$, *preussi* being 16.13% longer than *genderuensis*), bill depth (Wilcoxon rank sum test, $W = 300$, $P = 0.0004$, *preussi* being 9.96% thicker than *genderuensis*), bill width (Wilcoxon rank sum test, $W = 144$, $P < 0.001$, *preussi* being 11.39% wider than *genderuensis*), and tarsus length (Wilcoxon rank sum test, $W = 422.5$, $P = 0.010$, *preussi* being 6.31% longer than *genderuensis*; Tables 4 and 5). *C. r. preussi* and *C. r. parvirostris* differ significantly with respect to every variable from *C. r. reichenowi* (Tables 4 and 5). The two western taxa that are nearly indistinguishable in the PCA analyses, *C. r. preussi* and *Cinnyris reichenowi parvirostris*, can only be told apart by culmen length (Wilcoxon rank sum test, $W = 2341$, $P < 0.001$, *preussi* being 5.46% longer than *parvirostris*), which is the main character that was used by Eisentraut (1965) [98] to describe *parvirostris* as a distinct subspecies. Other separable groups included *C. r. reichenowi* and *C. r. genderuensis*, whose measurements differ only with respect to wing chord (Wilcoxon rank sum test, $W = 993$, $P = 0.005$, *genderuensis* being 2.81% larger than *reichenowi*) and culmen length (Wilcoxon rank sum test, $W = 1129.5$, $P < 0.001$, *genderuensis* being 7.29% longer than *reichenowi*).

Analysis of female sunbirds similarly separated individuals into these East and West groups, with some overlap between all populations. With respect to comparisons between *C. r. genderuensis* and *C. r. preussi*, populations were found to be separable in all pairwise comparisons except tail length (Wilcoxon rank sum test, $W = 131.5$, $P = 0.098$; Tables 4 and 5). The number of variables capable of separating populations was fewer for all but one comparison between female birds (*C. r. reichenowi* and *C. r. preussi* differ with respect to every variable; Table 4). All other populations had a reduced number of segregating characters, with the most similar populations being *C. r. reichenowi*/*C. r. genderuensis* and *C. r. preussi*/*C. r. parvirostris*.

Discriminant function analyses for males of the 3 best supported taxa—*reichenowi*, *preussi*, and *genderuensis*—recovered 2 main groups (*preussi* and *reichenowi*), with only one individual identified as a morphologically distinct third group (*genderuensis*). Two *genderuensis* were assigned to *preussi*, and all other individuals were assigned to *reichenowi*. Accuracy separating better-represented *reichenowi* and *preussi* is higher, with 95.1% of *preussi* and 98.1% of *reichenowi* assigned to the correct group based on morphological data. When randomly subsampling and re-performing the DFAs, we found that specimens could be identified to population with 89.1% accuracy, with the individual averages for *genderuensis* and *preussi* identification accuracy being 91.5% and 86.7%, respectively [71].

Like the male dataset, the female dataset was unable to discern genderuensis as a group separate from either *C. r. preussi* or *C. r. reichenowi* when the entire dataset was used. However, a test of only *C. r. preussi* and *C. r. reichenowi* was 96.1% accurate in separating these taxa based on morphological characters. When we repeated the random sampling method for *C. r. preussi* and *C. r. genderuensis*, we can separate females of these three taxa 85.4% of the time [71].

6.4.4 Ecological data

Populations differed with respect to several environmental variables, but *C. r. genderuensis* appeared to be from the most xeric localities and *C. r. preussi* from the least xeric [71]. Our models for past climate suitability increase the habitable area for each population in the eastern and western highlands, but also identify an area of suitability in the modern Central African Republic and the northern Democratic Republic of the Congo in the Holocene and Last Glacial Maximum (Figure 6.7). Populations appear to have been last connected during the Last Glacial Maximum, the most recent period where suitable conditions for these species were largest and most contiguous. The location of the suitable corridor differs for eastern and western populations; *C. r. reichenowi* predictions show an expansion across the southern Congo into Angola and up the coastal highlands towards Cameroon; *C. r. genderuensis* and *C. r. preussi* models show increased suitability eastward across the Central African highlands. All three populations show suitability in the interior Gabonese highlands near Makokou (an area where other highland taxa such as *P. insignis* have been recorded [43]), the Ituri region, and in localized parts of the southern Congo basin (*i.e.*, the northern edge of Katanga, DRC).

There is no significant difference between the ecological niche models and the null hypothesis of no ecological niche divergence for *C. r. genderuensis* and *C. r. preussi* (no tests with a significant P value; Table 5C). The niches of *C. r. genderuensis* and *C. r. reichenowi* are divergent when compared to null models of *C. r. genderuensis* ($P < 0.001$), but within the range of variation for *C. r. reichenowi* null models. Comparisons of *C. r. preussi* and *C. r. reichenowi* found that these species' ecological niches are significantly different when compared to the null distribution of *C. r. preussi* ($P < 0.025$), and near-significant when compared to the null distribution of *C. r. reichenowi* ($P = 0.034$). Reducing locality sets to the 80% of points that are closest to the niche centroid changes these overall results only with respect to the relationship between *C. r. reichenowi* and *C. r. genderuensis*, which are found to be significantly more similar than expected under the null hypothesis ($P < 0.010$ for both comparisons [71]).

6.5 Discussion

Our phylogenetic analyses recover clear separation between eastern and western *C. reichenowi* populations, with evidence for a single colonization event from East Africa westwards. Consistent with our hypothesis, we find evidence of diversification within the *C. reichenowi* complex forming three major groups, with *C. r. genderuensis* in the Adamawa

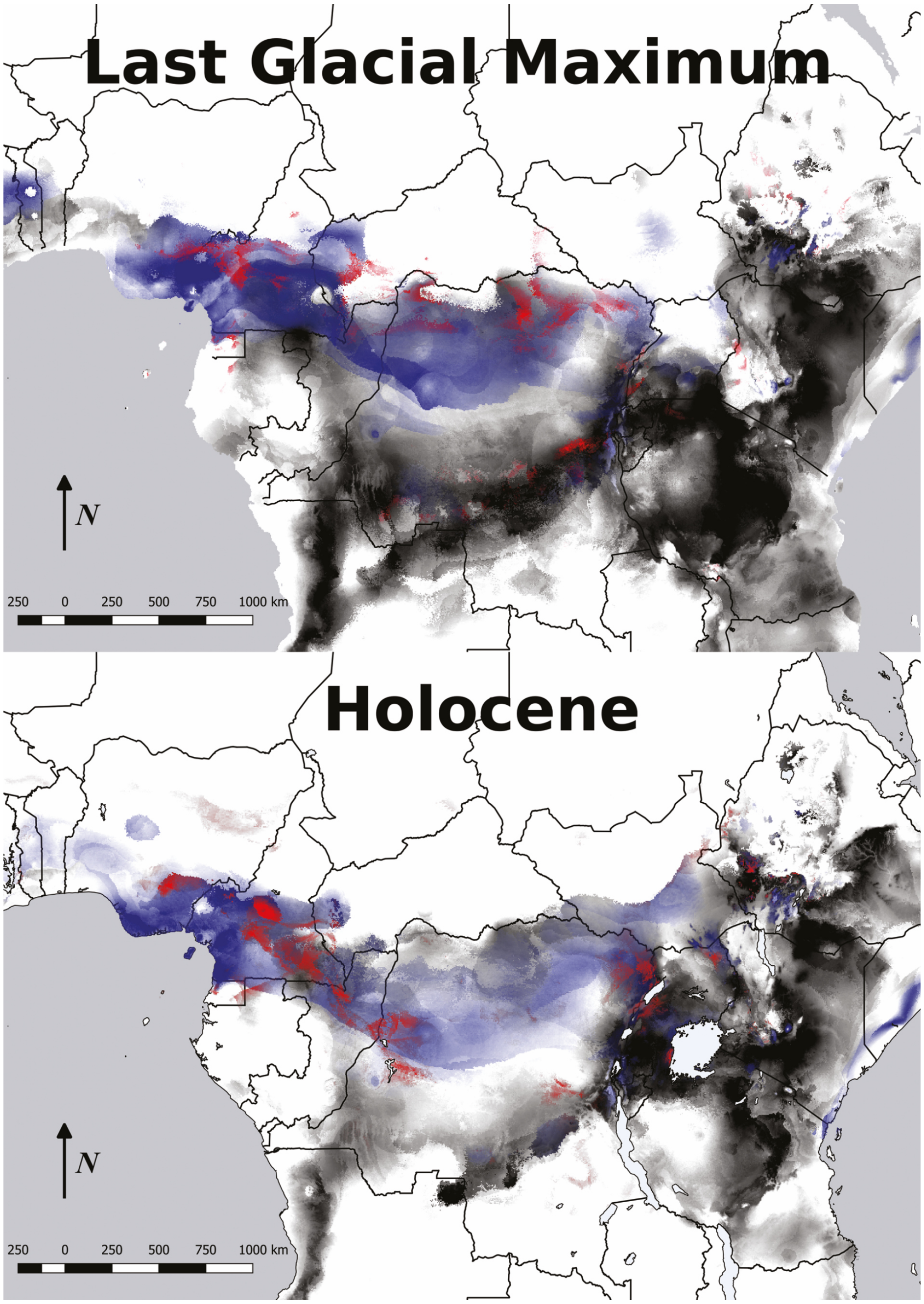

Figure 6.7: Projections of ancestral ranges in the Last Glacial Maximum and the Holocene with current geopolitical borders superimposed. *C. r. reichenowi* is in black (Mahalanobis distance 0–3 from centroid; fade 3–6), *C. r. genderuensis* is in red (Mahalanobis distance 0–8 from centroid; fade 8–20), and *C. r. preussi* is in blue (Mahalanobis distance 0–10 from centroid; fade 10–30). Note distances are not equal as models are based on different sample sizes and projections in past climates are unequal for different taxa; scales were selected to maximize visibility. Country names are provided in Figure 6.2.

highlands being more similar morphologically to the eastern *C. r. reichenowi* than to the adjacent, montane *C. r. preussi*. We did not find empirical support for ecological niche diversification between the adjacent populations of *C. r. genderuensis* and *C. r. preussi*, despite their parapatric distributions and the apparent preference of *C. r. genderuensis* for xeric plateaus in the interior of Central Africa. Our assessments of ecological niche evolution suggest niche differentiation is occurring with respect to *C. r. reichenowi* and *C. r. preussi* (with one of the two comparisons being significant in each comparison set). Our results strongly support two main ancestral populations and show three ancestral populations as the second most likely scenario (Figure 6.5). We confirm the biogeographic closeness of Mt. Cameroon and Bioko with respect to other highland areas, a pattern shared by other species inhabiting the highlands of Cameroon, Equatorial Guinea, and Nigeria (*e.g.*, Western Mountain Greenbul *Arizelocichla tephrolaema*, White-tailed Warbler *P. lopezi*) [43, 63].

Our gene flow analyses show evidence of some introgression between *C. r. genderuensis* and both *C. r. reichenowi* and *C. r. preussi*. This introgression, however, is most evident in the specimen that is missing data and obfuscating our analyses (FMNH 122395) or the specimen from the Bamenda Highlands (FMNH 273746) which is geographically between core *preussi* and core *genderuensis*. More research on intervening populations between Mt. Cameroon and the Bamenda Plateau is required to fully understand connectivity across these montane regions. Despite evidence for past introgression, it appears that differentiation between *C. r. genderuensis* and interior *C. r. preussi* is ongoing. Whether or not Cameroonian interior populations are diagnosable in the field without morphological measurements remains to be seen; while our inspections of museum specimens suggest that interior birds are more of a “golden green” than the coastal highland “emerald green” *C. r. preussi*, we have not quantified these differences.

6.5.1 Diversification dynamics

Ecological niche models indicate that *C. reichenowi* populations were in sympatry or local parapatry around the time of the Last Glacial Maximum (22,000 years ago). It is unclear whether this contact occurred via the highlands of south-central Africa, via the northern edge of what we consider Sub-Saharan Africa, or through a combination of these two routes (Figure 6.7). Under either scenario, as the climate warmed, distributions became more fragmented, approaching the current, modern distribution of the eastern and western groups. Species diversity in *Cinnyris* is centered in Eastern and Southern Africa, where they have adapted to numerous different habitats and niches. Within the "Double-collared" sunbirds, taxa have adapted to other drier habitats such as the miombo woodland (e.g., Western Miombo Sunbird *Cinnyris gertrudis*) adjacent to the highland regions, and multiple taxa have become restricted to individual remote highlands across the area of former suitability for *C. reichenowi*, such as Prigogine's Sunbird *C. prigoginei* endemic to the Marungu Highlands [224, 317].

Our mitochondrial genes indicate a divergence between eastern and western lineages 0.87 mya, despite potential distributional overlap as recently as 22,000 years ago and serious distribution fragmentation during the Holocene (6,000 years ago). The relatedness of Mt. Cameroon to Bioko reflects the island's isolation only 10,500 years ago [241, 301], and requires further insight into whether birds cross the channel periodically, given the monophyly of the SNAPP tree and the near sea-level distribution of *C. r. preussi* on the windward slopes of Mt. Cameroon 35 km from populations on Bioko [308]. Mitochondrial dating of the divergence between eastern and western populations of *C. reichenowi* near-coincides with estimates of a large increase of Antarctic ice volume during the mid-Pleistocene climate transition [100]. More investigation of the timing of population isolation in the Cameroon highlands is warranted, and requires more, higher quality sampling and caution regarding skewed divergence times due to potential fixation from small effective population sizes during the fragmentation of populations during glacial cycles. More extensive genomic data will also elucidate if climatic cycling (and which climatic cycles) coincided with diversification events and contribute to effective population size fluctuations within *C. reichenowi* and within the genus *Cinnyris* as a whole.

A mystery arising from this study is the lack of *C. reichenowi* from the southern highlands of Africa. According to mitochondrial data, *C. reichenowi* is sister to Southern Double-collared Sunbird *C. chalybea* of South African fynbos and highlands [45], with a large disjunction between this species and the nearest populations of *C. reichenowi* in the Albertine Rift. If the southern highlands were used to colonize the western part of the African continent, then it appears that all geographically intermediate populations have since gone extinct [2]. However, no fewer than eight additional double-collared *Cinnyris* occur in south-central Africa from Angola to Malawi and Kenya, including the Montane Double-collared Sunbird *C. ludovicensis*, found in Angola (nominate subspecies) and disparately in Malawi and Zambia (*whytei*, sometimes elevated to species rank) [45]. Several other avian taxa occurring in both East and West Africa also have populations in Angola, with limited evidence that colonization across Africa occurred via Angola for some groups [349]. It is also possible that these other *Cinnyris* species would have provided a biotic barrier via competition, thus preventing *C. reichenowi* from colonizing via the south. This scenario would further support the idea that these species colonized across the northern Congo basin, where some outlying populations still remain (*e.g.*, *C. r. genderuensis* in the western Central African Republic and *C. r. reichenowi* in the Imatong Mountains of South Sudan and Uganda).

Considering *C. reichenowi* in this greater radiation provides further insight into potential mechanisms for the separation of *C. r. genderuensis* from adjacent populations of *C. r. preussi*. The Rift mountains possess multiple *Cinnyris* sunbird species along with larger sunbirds from other genera [198, 317]. Several larger species are sympatric with *C. r. reichenowi*, including Rwenzori Double-collared Sunbird *C. stuhlmanni* and *C. regius*. At the fringes of the distribution for *C. reichenowi*, there are other highland forms that are locally sympatric or geographical replacements, most notably the Eastern Double-collared Sunbird

C. mediocris. The niche space for sunbirds is significantly more packed locally and regionally in Eastern Africa than it is in Central and Western Africa, where the only other strictly montane sunbird species are the more distantly related Ursula's Sunbird *C. ursulae* and the long-billed Cameroon Sunbird *Cyanomitra oritis*, itself presumably sister to the East African Blue-headed Sunbird *Cyanomitra alinae*. In the xeric Adamawa, there are no other montane "Double-collared" sunbirds, and *Cinnyris r. genderuensis* is thus relatively unique in these habitats (though there are other *Cinnyris*, *e.g.* Olive-bellied Sunbird *C. chloropygius* and Orange-tufted Sunbird *C. bouvieri*). In the eastern part of its distribution, the small-billed *Cinnyris r. reichenowi* occurs largely below the elevational zone of the large billed, alpine *C. stuhlmanni*, and locally co-occurs with other *Cinnyris* such as *C. regius* and possibly Rockefeller's Sunbird *C. rockefelleri* [317]. In the western montane regions, these species are replaced by *Cinnyris r. preussi*, the largest billed of all *C. reichenowi* populations and the largest high-montane *Cinnyris* in the Cameroon Line [43]. Countering this propensity for larger bill evolution is that birds on Bioko ('*parvirostris*') possess bill lengths significantly smaller than core *preussi* and significantly larger than *genderuensis* (Table 4) [71]. The reasons for this disparity are not known, but may be related to the insular nature of Bioko.

The null expectation for any allopatric population is niche conservatism with respect to historical conditions [267]. If we operate on the assumption that *C. r. reichenowi* represents the ancestral state for the species, then only *C. r. preussi* has diverged in some regard. *C. r. genderuensis* appears to inhabit more xeric areas when compared to montane regions, but it has not diverged in bill morphology and it is not divergent according to niche equivalency tests. Populations of *C. r. reichenowi* in the Imatong Mountains of South Sudan and the mountains of Kenya warrant further investigation to determine if ecological diversification is also occurring in the East. More rigorous studies are required to understand whether these morphological and ecological differences are truly driven by biotic interactions or if they are the result of more random evolutionary processes.

6.5.2 Taxonomic classification

Given the inherent genetic structure within these populations coincident with their geographic separation, we recommend the recognition of two species and three taxa of *Cinnyris* sunbird in the place of *C. reichenowi* sensu lato. We refrain from assigning these names the "Double-collared" moniker, as this feature is absent for some "Double-collared" species (*e.g.*, Neergaard's Sunbird *C. neergaardi*) and can lead to confusion between taxa.

Rift Sunbird *C. reichenowi* [311]: occurring broadly across eastern Africa, from the Albertine Rift to the highlands of Kenya. Monotypic.

Volcano Sunbird C. preussi, consisting of the following two subspecies: **Genderu Sunbird *C. p. genderuensis*** [293] restricted to the greater Adamawa Plateau region of Cameroon, the Central African Republic, and likely occurring in northeastern Nigeria; and the nominate **Volcano Sunbird *C. p. preussi*** [292] widespread in the humid volcanic highlands of Cameroon, Equatorial Guinea (Bioko Island), and Nigeria. Bioko *parvirostris* [98] is best considered a synonym of *preussi*, as it is only distinguishable by bill and tail length and is genetically indistinguishable from adjacent mainland populations.

There is still difficulty in knowing the range limits and exact distribution of *C. p. genderuensis* and *Cinnyris preussi preussi*, but it is clear that these taxa have diversified morphologically, and ecologically, and possess different genetic signatures that, despite evidence of admixture, fall into discrete monotypic clades. We refrain from recognizing these populations as full species at the present time, but note that *genderuensis* may be worthy of species rank pending additional research in the northern Cameroon contact zone.

6.6 Future research

This research focused on elucidating the relationships between western populations of *C. reichenowi* sensu lato, in large part to determine whether *C. p. genderuensis* is an ecomorph of *C. p. preussi* or its own, distinct taxon. However, this study has not emphasized coverage of the East African *Cinnyris*, including outlying populations of *C. reichenowi*. The population of *C. reichenowi* is known from the Imatong Mountains of South Sudan and northern Uganda, where they occur on small, more xeric ridges that are geographically isolated from the main, humid mountain ranges of the Albertine Rift. There is also a population of *C. reichenowi* that occurs predominantly in Kenya and eastern Uganda that abuts several other *Cinnyris* species, including the similar *C. mediocris*. Whether there is ongoing diversification in eastern *C. reichenowi* is unknown. Birds in Kenya were originally described based on one specimen as the race *kikuyuensis* [240], a race which has since been synonymized with *reichenowi* [120]. Given the amount of structure within western *C. reichenowi* sensu lato, a more comprehensive analysis of all "Double-collared" sunbirds is warranted, especially the smaller birds found in Kenya, Sudan, and adjacent eastern Uganda [45].

6.6.1 Understanding Afromontane diversification

This research has reinforced the finding that museum toepads can be used to facilitate work on gene flow and species limits. Most African specimens were collected before the practice of gathering tissues and other associated metadata with a specimen. Thus, many specimens from Africa do not have the modern genetic material to include in studies. The use of next generation sequencing technologies allows for the use of these historical toepads and thereby fills in some sampling gaps. These historical specimens can become valuable extended specimens [360] documenting genotypic variation as well as phenotypic variation across geography to shed more light on speciation dynamics and connectivity across the continent.

This case study illustrates the complex nature of speciation events across Afromontane ecosystems and is a demonstration of niche shifts occurring in species that have colonized across the African continent. Many Afromontane disjunct taxa appear to have conserved niches, occurring only in montane forests (*e.g.*, White-breasted Robin-Chat *Cossyphicula roberti*). But like *C. preussi*, there are other Afromontane taxa that illustrate similar high and low elevational differentiation that has been described at the subspecific level, namely Elliot's Woodpecker *Dendropicos elliotii*, with nominate lowland and highland *johnstoni*, sometimes regarded as specifically distinct, and Black-throated Apalis *Apalis jacksoni*, with lowland nominate and highland *bambuluensis*. The presence of these phenotypically similar but genetically differentiated montane and lowland populations is worth investigating in other populations. A better idea of the genetic structure within and between species that occupy different mountain ranges and different elevation bands in the Afrotropics is necessary for fully understanding the evolutionary dynamics across sub-Saharan Africa.

6.7 Supplementary material

Supplementary material is available from the American Ornithological Society, specifically from the publication *Ornithology*.

6.8 Acknowledgments

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6.10 Ethics statement

All specimens used in this paper are archived museum specimens available for research.

6.11 Data availability

Analyses reported in this article can be reproduced using the codes and non-genetic data provided by Cooper et al. (2021). Genetic sequences are available on GENBANK under Bioproject PRJNA678703: SAMN16810525-SAMN16810548.

6.12 Disclaimer

This chapter is a peer-reviewed publication in *Ornithology* [72]. This chapter has been adapted for the sole purposes of meeting the requirements of a University of Chicago PhD.

CHAPTER 7

NICHE THEORY AND ITS RELATION TO MORPHOLOGY AND PHENOTYPE IN GEOGRAPHIC SPACE: A CASE STUDY IN WOODPECKERS (PICIDAE)

7.1 Abstract

Ecogeographic analyses have recovered common environmental trends with respect to morphology; however discrepancies among trends exist. Hypothesized reasons for these divergences vary, but most relate a taxon's morphology to its ecological niche. Morphology is known to diverge when species co-occur with competitors or predators and when species occur across different habitats and environments. A less understood divergence from ecogeographic trends is niche fixation, wherein species become locked into particular niches due to their community interactions or foraging ecology. A form of niche fixation has been hypothesized in the theory of interspecies social dominance mimicry (ISDM), in which mimics maintain relatively constant size ratios with models to perpetuate their mimicry. If true, mimics should display variation and trends in tandem with their models. Here, I use mass as a proxy for body size and examine ecogeographic trends in two sets of woodpeckers (Picidae): a Nearctic group which has been reported to interact via ISDM, and a Neotropical group which, based on similar appearances and overlapping distributions, is a potential ISDM system. I found ecogeographic trends suggestive of differential evolutionary responses, and I found evidence against niche fixation in the Nearctic clade. The Neotropic clade showed limited evidence for tandem size evolution between models and mimics, but inconsistencies in the size ratios between mimic and model populations. Here, I discuss the implications of observing divergent ecogeographic trends within mimicry systems, with specific emphasis on how environment, ecology, and community interactions guide evolution.

7.2 Introduction

Three definitions of niche are broadly used to define species' interactions, ecologies, and spatial distributions: the Grinnellian niche [146], where a taxon's distribution is limited to a suite of environments and habitats to which it is best suited morphologically and behaviorally; the Eltonian niche [101], where a taxon's distribution depends heavily upon access to resources and related interactions with syntopic (*i.e.* co-occurring) taxa over resources; and the Hutchinsonian niche [174], where n number of biotic and abiotic variables are represented as n axes and a taxon's distribution is the spatial area corresponding to a hypervolume of suitable conditions on these axes. While all of these perspectives provide overlapping views, each offers its own specific insights on factors that may limit or constrain species ecologically. Of these definitions, the Hutchinsonian niche is the one most often presented as a broad definition for determining species' distributions and is often used to create 'scenopoetic' environmentally trained ecological niche models [268, 324, 325]. Given that both amensal (*i.e.* antagonistic) and commensal (*i.e.* benefiting from co-occurrence) relationships can be hypothesized by a taxon's absence/presence in areas suitable for other taxa, spatial projections of the Hutchinsonian niche are often regarded as projections of the Grinnellian niche as well, and thus are considered a representation of the environments and the habitats that are suitable for a species [5, 268, 323, 326].

While such models of environment and basic land cover are sufficient for describing the basic ecological and spatial trends of species, their usefulness for describing biotic interactions is still debated. Some biotic interactions may not be informative for estimating distributions when assessed over broad geographic extents; conversely, these same interactions may be integral to a species' local occupancy and be predictive of occurrence over smaller spatial extents (*i.e.* the Eltonian noise hypothesis sensu Soberón and Nakamura [324]). Several recent studies have shown improvements in distribution models using explicit biological variables, demonstrating that distribution estimates can be improved by including data for co-occurring species or habitat information [6–8, 74, 155]. These models deal explicitly with the spatial correlation between a study taxon and different species or habitats, thereby addressing species' interactions at individual localities [101, 323, 348]. Using niche modeling techniques, commensal co-occurrence is detectable, but other ecogeographic interspecies interactions can be difficult to assess. One example of an important interspecies relationship that might affect a species' niche and is difficult to include in spatial models is mimicry. Multiple types of mimicry exist in nature, with two predominant categories: Batesian mimicry, where a taxon mimics one or more 'avoided' (*i.e.* aggressive, toxic, etc.) taxa to discourage depredation and/or aggression on itself despite lacking the properties discouraging amensal interactions [21]; and Müllerian mimicry, where multiple taxa with similar adaptations discouraging depredation and/or aggression evolve similar phenotypes [246].

Woodpeckers (Aves: Picidae) appear to contain multiple recurrences of Batesian mimicry in the form of interspecies social dominance mimicry (ISDM). In these cases, a mimic is hypothesized to have evolved to copy the phenotype of a more aggressive co-occurring model species to facilitate foraging while minimizing antagonistic interactions either with the model species or with the model species and third party observers [89, 276, 356]. Recent work has argued that ISDM systems are widespread in birds [278], and that ISDM systems can have more than one sympatric mimic converging on the phenotype of a larger, more aggressive taxon [27]. Preliminary analysis of mass within ISDM complexes has revealed a trending of mimics to be ca 55–60% of the mass of their models [278]. This indicates that selection on morphology may be concurrent with selection on phenotype, leading to the hypothesis that maintaining specific size ratios is imperative for maintaining mimicry dynamics [278]. The relationship is suggestive of an interlocked Eltonian niche dynamic that may lead to fixation in a species' niche, possibly for both the mimic and the model, with respect to maintaining a specific size ratio.

Spatial recovery of an Eltonian interaction is not new: previous studies have demonstrated character clines across contact zones in complexes that exhibit spatially localized sympatry [110, 140, 202, 239, 300]. These studies focus heavily on character displacement, and demonstrate that taxa diverge in specific character traits to reduce competition in sympatry. These systems, however, are not mediated by mimicry. ISDM systems are different in that competition leads to phenotypes and morphologies that allow syntopy. Even if species partition available resources from the outset, there appears to be an inherent benefit in converging on a dominant competitor's phenotype at a specific size ratio [278]. Thus, the difference in size between taxa may not be the maintenance of independently derived niches in the Grinnellian sense, but a novel Eltonian relationship reducing competition for non-dominant species. ISDM systems represent opportunities to view the ecological niches of sympatric taxa while correcting for spatial trends.

While a thorough ecogeographic study of *Picoides* sensu lato exists, it is scenopoetic in nature, and focuses on the relationships between observed morphological variation and known climatic conditions [183]. Re-examining these systems within an ISDM framework allows a restructuring of the questions, to ask if the response of the mimic conforms to the same environmental trends as the model or varies from the expectation under ISDM theory, thus revealing that other ecological needs may be mediating size through space. For example, if a species (mimic or model) maintains a similar size across all environments and habitats, it is possible that there is significant Grinnellian selection to maintain a morphology that is suited to a certain foraging behavior or habitat. Similarly, if a species' morphology varies greatly with respect to environment across space, we can deduce that this is a response to Hutchinsonian factors, and that certain morphological trends may exist to increase survival in local climates [28, 183]. Lastly, while we may not possess the capacity to discern interspecific interactions according to the Eltonian niche for a model species, we should be able to determine whether mimic species are 'fixed' in a particular Eltonian relationship based on how closely they maintain a specific size ratio with their presumed model over geographic space. A well-defined Eltonian niche in this sense would erase evidence of other evolutionary drivers on the mimic due to high correlation with the geographic trends observed within the model taxa. The broad distributions of woodpeckers enable the close examination of these trends, as many mimics co-occur with their models across a wide range of environments and habitats, allowing for trends to be dominated by any of the three ecological niche definitions.

Here, I compare two sets of ISDM woodpecker complexes to study these potential relationships, using mass as a proxy for overall body size. The first complex is restricted to the Nearctic, and consists of two phenotypically near identical, but distantly related, black-and-white woodpeckers formerly placed in *Picoides*: Downy Woodpecker *Dryobates pubescens* and Hairy Woodpecker *Leuconotopicus villosus* [121, 130, 276, 278, 309, 361, 362]. These species are broadly sympatric across North America, from Alaska to far northwestern Mexico and Florida. Allopatric populations of the larger model taxon *L. villosus* exist in areas that lack *D. pubescens* from Mexico southwards through Panama [181, 182]. The two species exhibit geographic variation in relation to overall size and mass, with documented trends associated with climate in *D. pubescens* [183] and with southernmost *L. villosus* populations being smaller than northern populations [182]. *Dryobates pubescens* and *L. villosus* differ from each other with respect to foraging ecology, with *L. villosus* preferring larger branches and trunks than the smaller *D. pubescens* [181, 182]. The foraging ecology of *D. pubescens* is similar to closely related taxa, but it differs from these species with respect to environment and habitat [181, 220, 221]. *Leuconotopicus villosus* exhibits microhabitat preference for larger trunks and limbs throughout its North American range [182] and it appears to excavate more than its close relative, Arizona Woodpecker *L. arizonae* [187]. The second ISDM system is restricted to the Neotropics, and contains multiple geographically overlapping black-and-white woodpeckers of the genera *Campephilus*, *Celeus*, and *Dryocopus* [27, 167, 278]. Specifically, multiple species of large *Campephilus* woodpeckers all co-occur with smaller, similarly-patterned Lineated Woodpecker *Dryocopus lineatus* populations [167]. In southeastern Brazil, populations of Cream-backed Woodpecker *Campephilus leucopogon* and *Dryocopus lineatus* co-occur with another small black-and-white woodpecker that appears to be part of this mimicry dynamic as well. This species, the Helmeted Woodpecker *Celeus* *galeatus*, is so similar in plumage to the previous two species that it was erroneously believed to be in the genus *Dryocopus* until recently [27].

Phenotypic variation within *Dryocopus lineatus* appears to parallel larger sympatric *Campephilus* [27, 167, 278], and gives credence to the notion that phenotype is controlled by an Eltonian relationship. *Campephilus* woodpeckers vary in mass, and similar phenotypes are parapatric (*i.e.* minimally overlapping and replacing each other) in distribution, creating a mosaic of different models for the mimic species to copy. While we do not have nearly as much data relating to foraging ecology for large Neotropical woodpeckers as for *Picoides* sensu lato, the available information suggests that most *Campephilus* and *Dryocopus* forage in a similar manner, taking advantage of insects from the surface to fairly deep within the trunks of trees [1, 197, 227, 313, 320, 373]. Given the paucity of data regarding most of these large Neotropical woodpeckers, I have focused on two of the most widely sampled *Campephilus* (Pale-billed Woodpecker *C. guatemalensis* of North and Central America and Crimson-crested Woodpecker *C. melanoleucos* of Panama and eastern South America) and their widespread presumed mimic, *Dryocopus lineatus* (which occurs from northern Mexico to Argentina). I have excluded other similarly plumaged *Campephilus* models and potential *Celeus* and *Dryocopus* mimics that are less well represented in museum collections, notably: Powerful Woodpecker *Campephilus pollens* (Andes Mountains); Robust Woodpecker *C. robustus* (southern Brazil and adjacent Paraguay and Argentina); Guayaquil Woodpecker *C. guayaquilensis* (western Colombia, Ecuador, and Peru); *C. leucopogon* (Bolivia, Paraguay, and Argentina); *Celeus galeatus* (southern Brazil and adjacent Paraguay and Argentina); and Black-backed Woodpecker *D. schulzi* (Bolivia, Paraguay, and Argentina).

If mimics are morphologically locked in an Eltonian niche with respect to their sympatric model taxa, then geographic trends of mimic mass should follow those of their models. While this correlation could also exist from similar Hutchinsonian dynamics, the magnitude of the ecogeographic trends can be assessed to see if it fits the predictions of Prum [278]. Different data trajectories between the taxa, however, will allow us to hypothesize what aspects of niche biology are affecting species' masses. If taxa are constrained by foraging ecology, their masses should be relatively constant due to ecological constraints on their foraging behavior and therefore weakly correlated to their environment. Conversely, if models are responding mostly to scenopoetic (Hutchinsonian) factors, then mass should significantly track environmental conditions. Using this framework, we can distill whether morphological character fixation is occurring within ISDM complexes, and we can begin to understand other aspects of niche dynamics with respect to basic community interactions.

7.3 Material and methods

Data were mined online and, after minimal reformatting, entered into a workflow for processing and analyzing these data in R that is available via the Dryad repository. As elucidated below, this pipeline takes the downloaded mass data and reduces the data by removing significant outliers, juvenile birds, etc. before combining it with data extracted from environmental data rasters and clustering points by biogeographic region. The code subsets and analyses both the Nearctic and Neotropical datasets, includes everything necessary to perform all statistical analyses, and includes the code to recreate every figure with the exception of Figure 7.1. Georeferenced mass data were downloaded directly from VertNet (a database of vouchered biodiversity records and their associated metadata, `http://www.vertnet.org`; Appendix) on 17 November 2016. Data were parsed to include only the relevant study taxa that possessed greater than ten georeferenced occurrences with recorded mass (*i.e.* specimen records with coordinates and mass information available; Appendix). These data were imported into *R* 3.4.4 [285] and manipulated with the packages *ggplot2* [369], *maptools* [37], *raster* [158], and *rgdal* [34]. Given the numerous outliers that existed in the mass dataset, all species were restricted to non-juvenile birds with masses within two standard deviations of the mean for that species. This procedure clipped extreme outliers, while preserving the tails of the distribution where true morphological variation may be represented. Thus, all specimens < 10 g and all *Dryobates pubescens* > 40 g were removed from the dataset. Specimens under < 10 g were removed to ensure that no juvenile or immature birds were included, while the 40 g threshold was enforced for *D. pubescens* as this is larger than any known populations and indicative of probable identification or weighing error in the collections [181]. One additional record (KU 95783) was removed as it was the only record from its geographic area and appears to be a fledgling (heavy molt, smooth ovary, unossified skull, collected 22 May 2003), despite being > 10 g and not being labeled as a juvenile within the database. 81.8% of records had a posted coordinate uncertainty, with an average uncertainty of 8.2 km. Points with uncertainties of greater than 25 km were removed from the dataset to limit the effects of potentially inaccurate coordinates; this step affected only *Dryobates pubescens* and *Leuconotopicus villosus*, and reduced the number of points used for each by 15 and 34 points, respectively.

Climatic data for these species were drawn from five datasets of two factors from the WorldClim 1.4 database [161] that have been shown to affect bird distributions in North America [302]: average temperature of the warmest quarter, average temperature of the coldest quarter, average rainfall in the driest quarter, average rainfall in the wettest quarter, and cumulative precipitation. The WorldClim 1.4 data covers the time period of 1960–1990, which temporally encompasses 23% of the specimen data used explicitly (whereas the WorldClim 2.0 database temporally includes only 11% of all specimen data). A total of 81% of the records come from 1990 or earlier. While morphological changes in populations have been documented within time periods as short as 30 yr [50], I evaluated all records with the WorldClim 1.4 dataset as insufficient data exist to determine if localized mass evolution is occurring in these woodpeckers as the climate warms. The WorldClim 1.4 data exists in a 2.5 arcminute grid, which is 4.6 km at the equator, compared to the average spatial uncertainty of specimen records of 8.2 km. Such spatial inaccuracies may affect the extraction of environmental data for the localities, but these effects were considered minimal due to the spatial corrections that were employed and due to the broad distributions of the species studied in depth [167]. Specimen records that possessed ‘NA’ values for climate factors (*i.e.*

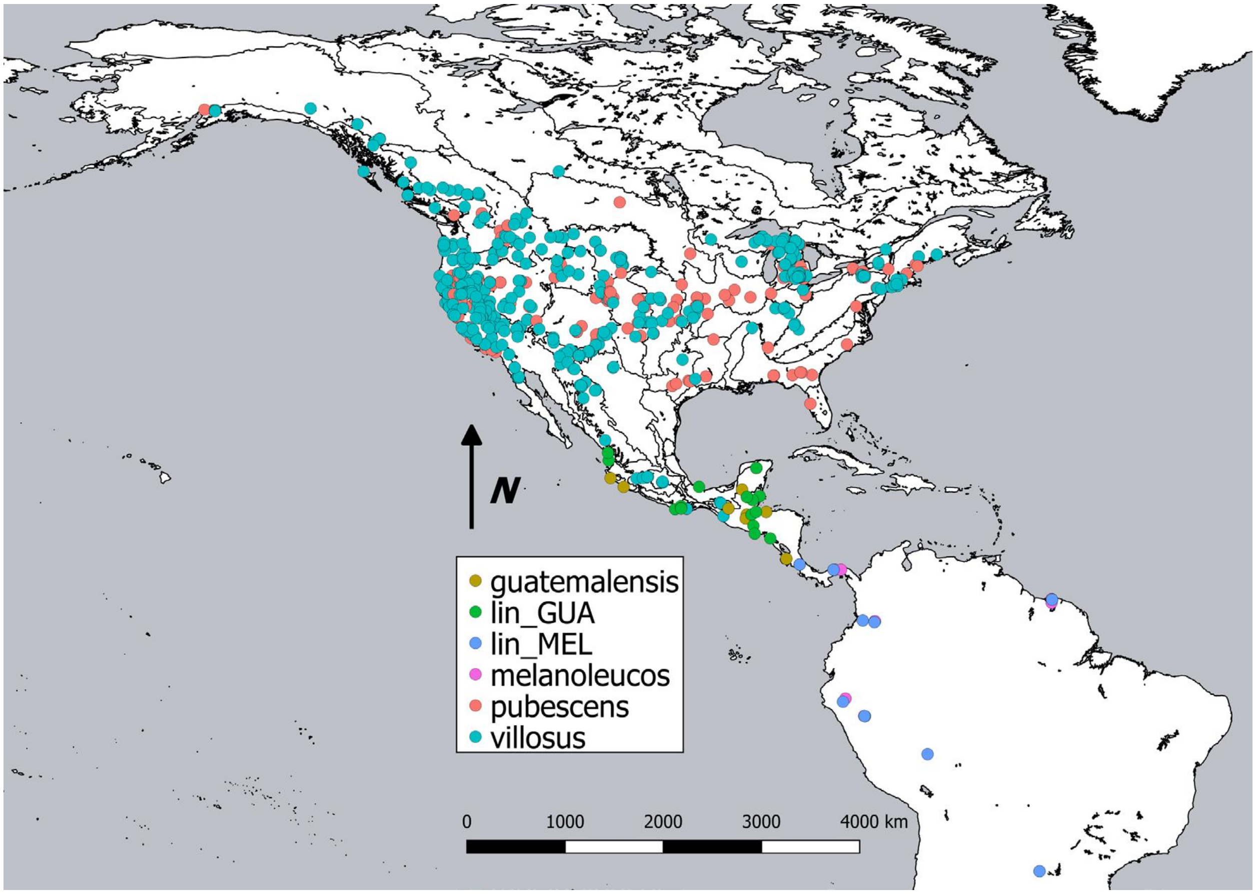

Figure 7.1: A map of georeferenced specimen records that were used in this study for *Campephilus guatemalensis*, *C. melanoleucos*, *Dryocopus lineatus*, *Dryobates pubescens*, and *Leuconotopicus villosus*. The annotations of 'lin-GUA' and 'lin-MEL' correspond to populations of *D. lineatus* that are sympatric with *C. guatemalensis* and *C. melanoleucos*, respectively. Polygons overlaid on North America are Bird Conservation Region boundaries [32]. Map created using data layers from NaturalEarthData.com and QGIS 2.8.6 [281].

records from outside the extent of the environmental data rasters) were removed from the analysis. In addition to these layers, another layer of 'environmental variation' was created by means of principal components analysis (PCA [188]) of climactic conditions at occurrence localities using the built-in *R* function 'princomp' (R Core Team). Analyses were made with PC1 (which explained 57.5% of the variance, mostly driven by the annual precipitation and precipitation of the wettest quarter) and PC2 (which explained 22.4% of the variance, mostly driven by the mean temperature of the warmest quarter).

Nearctic woodpeckers were overlaid on the Bird Conservation Region (BCR [32], Fig. 7.1) shapefile to aggregate records by ecologically similar areas. This dataset includes 66 expert-defined ecological regions that are inclusive of regional bird communities in similar habitats. Ecoregions are numbered from northwest to southeast and cover the entirety of the Canada, the United States, and Mexico. As this region is inclusive of the study area for *Dryobates pubescens* and *Leuconotopicus villosus*, all records that fell outside of defined BCR regions were removed from the analysis. Overviews of these data revealed that most United States records affected by this step were in the pelagic zone of the Great Lakes, likely representing erroneous coordinates or coordinates that appear pelagic due to a lack of precision and/or accuracy. This procedure also excluded populations of *L. villosus* from the Bahamas and from Guatemala southwards; these exclusions do not affect the comparisons as none of these populations are sympatric with *D. pubescens*, and therefore exist in different picid communities. Data that remained for these species were concentrated in the western and central United States; there was little data from eastern North America away from New England and Michigan, especially for *L. villosus* (Fig. 7.1). The reasons for this regional bias are complex, but include a lack of georeferencing and mass data for older specimens and individual collections' data sharing policies (some museums do not share data or only serve partial datasets online that may exclude coordinates or mass).

Neotropical species' ranges were estimated using generous kernels limited by major biogeographic regions around the species' known distributions following the methods of Cooper and Soberón [73]. These estimates were intentionally made broader than range maps available online to account for potential regions of dispersal within the mimic and model taxa [298]. These dispersal areas were 'clipped' to major biogeographic barriers (*i.e.* mountains, rivers, etc.) or placed a significant distance (*e.g.* 100 km) from known occurrences in homogeneous terrain. Points of each species were then overlaid on the map to determine which populations are sympatric, with these points used for mass comparisons. Any points outside of this kernel – whether of the model or the mimic – were ignored to ensure the study was focusing on a concise geographic area of known occurrence and to avoid potentially misidentified or mislabeled specimens. *Dryocopus lineatus* records were separated into two populations, those sympatric with *Campephilus guatemalensis* (*i.e.* northern) and those sympatric with *C. melanoleucos* (*i.e.* southern), for geographically-corrected comparisons of mass.

After data cleaning, 1241 georeferenced specimen records with mass remained, specifically: 27 *Campephilus guatemalensis*, 13 *Campephilus melanoleucos*, 457 *Dryobates pubescens*, 31 *Dryocopus lineatus* (northern), 14 *Dryocopus lineatus* (southern), and 699 *Leuconotopicus villosus* (Appendix). Sufficient data existed for the Nearctic dataset for an analysis of covariance (ANCOVA [84]) and linear model (LM) analyses to be performed with respect to environmental variables. While residuals were left-skewed, ANCOVA can be robust to some violations of non-normality [245]. Given the paucity of data from most of the Neotropic system, adjacent populations were compared using Wilcoxon tests [84] and boxplots, with regressions performed only on latitude (based on the importance of this variable for Nearctic species). I also performed LM models of these species to determine if any trends were apparent with the available data. I directly compared all regression slopes using Welch's *t*-tests [84]. Values are presented with a confidence interval of ± 2 standard errors.

7.3.1 Data deposition

Data are available from the Dryad Digital Repository: `http://dx.doi.org/10.5061/dryad.d6d5011` [68].

7.4 Results

7.4.1 Analysis of Nearctic woodpeckers

Geographic comparisons of the Nearctic black-and-white woodpeckers that account for habitat, latitudinal trends, and climatic correlates revealed that mass of *D. pubescens* and *L. villosus* vary with Bird Conservation Region (BCR), but *D. pubescens* is always smaller than its model, *L. villosus* (Wilcoxon rank sum test, $W = 28.5$, $P << 0.005$, mimic/model ratio = 0.39; Fig. 7.2). Regressions of average mass per BCR confirm that mass of *D. pubescens* increases as mass in *L. villosus* increases ($R^2 = 0.46$). The slope of this relationship (*i.e.* the slope of mimic/model ratios in multiple populations of *Dryobates* and *Leuconotopicus*; 0.18 ± 0.08) rejects the hypothesis of trending in tandem that would be expected for these species given the reported slope of the mimic/model ratios (0.56 ± 0.04) for ISDM complexes suggested by Prum [278] (Welch's t-test, $t = –8.52$, $df = 29.56$, $P < 0.05$; Fig. 7.3). An analysis of covariance determined that both species increase in mass as latitude increases, but the two species possesses distinct slopes with respect to latitude ($F(2, 1153) = 8138, P << 0.005$). The relationships, while correlated, are operating independently (Fig. 7.4). Regression equations calculated for the data revealed that both latitude and the mean temperature of the coldest quarter explained much of the variance within the data for *L. villosus* only, with latitude (*D. pubescens*: $R^2 = 0.07$; *L. villosus*: $R^2 = 0.58$) performing better than regressions with respect to coldest temperature (*D. pubescens*: $R^2 = 0.03$; *L. villosus*: $R^2 = 0.32$) or overall environmental variation (principal component 1: *D. pubescens*: $R^2 < 0.01$; *L. villosus*: $R^2 = 0.05$; principal component 2: *D. pubescens*: $R^2 = 0.03$; *L. villosus*: $R^2 = 0.16$). Longitudinal analyses performed poorly in describing overall geographic variation (*D. pubescens*:

$R^2 = 0.04$; *L. villosus*: $R^2 = 0.06$).

7.4.2 Analysis of Neotropical woodpeckers

The difference in size between *Campephilus guatemalensis* and *C. melanoleucos* was found to be insignificant (Wilcoxon rank sum test, $W = 231, P = 0.11$), with *C. guatemalensis* averaging 95% the size of *C. melanoleucos*. Both species were significantly larger than their sympatric populations of *Dryocopus lineatus*, with *C. guatemalensis* (Wilcoxon rank sum test, $W = 826, P << 0.005$) possessing a mimic/model ratio of 0.67 and *C. melanoleucos* (Wilcoxon rank sum test, $W = 8.29, P << 0.005$) possessing a mimic/model ratio of 0.80. Similarly, the population of *Dryocopus lineatus* sympatric with *C. guatemalensis* is significantly smaller than the population of *D. lineatus* sympatric with *C. melanoleucos* (Wilcoxon rank sum test, $W = 38, P << 0.005$, ratio = 0.79; Fig. 7.5). General examinations of mass in comparison to latitude of the Neotropical woodpeckers recovered a dichotomy, with a response demonstrated by northern populations but not by southern populations. The overall trend of *D. lineatus* was a large increase in mass going southward, with the smallest birds near 25°N and the largest birds near 10°S. Similarly, *Campephilus guatemalensis* was largest near the southern end of its distribution in northern Costa Rica, where they appear to be locally sympatric or parapatric with the northernmost populations of *Campephilus melanoleucos* (eBird 2012). Dividing the *Dryocopus lineatus* populations allowed for comparisons of the slopes from within each geographic region, revealing that latitudinal trends are roughly parallel between *Campephilus* and *Dryocopus* (Fig. 7.6). The strongest relationship was recovered for *C. guatemalensis* ($R^2 = 0.33$), with lesser responses observed for *C. melanoleucos* ($R^2 = 0.24$) and northern populations of *D. lineatus* ($R^2 = 0.27$). Almost no trend was recovered for southern *D. lineatus* ($R^2 = 0.02$). Both relationships were found to be indistinguishable using *t*-tests (Welch's *t*-tests, northern: $t = -0.927$, df = 26.04, $P > 0.05$; southern: $t = -1.42$, df = 12.20, $P > 0.05$), but the relationships between *C. guatemalensis* and *D. lineatus* were significantly different when compared using ANCOVA

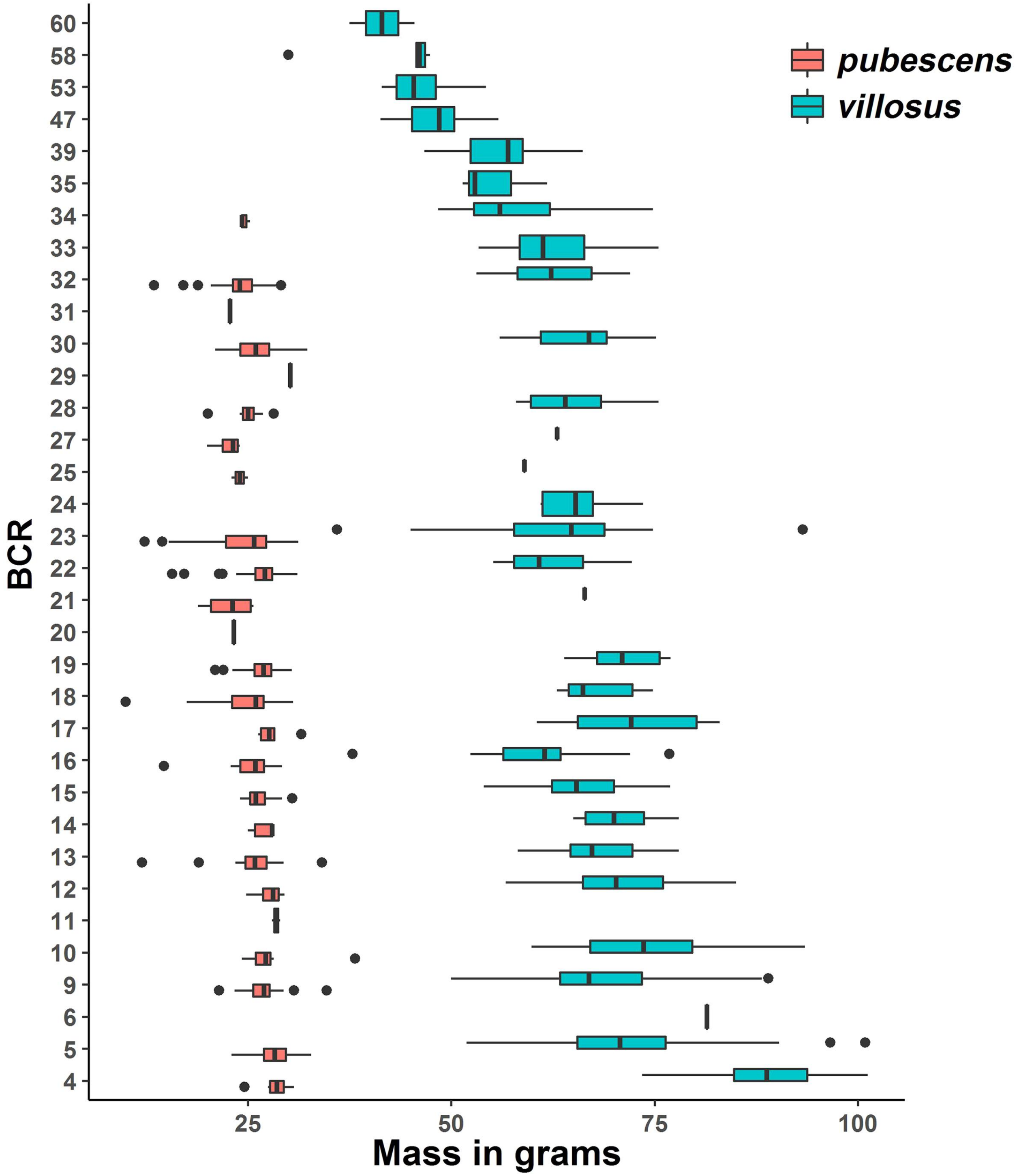

Figure 7.2: Boxplots of mass of *Dryobates* and *Leuconotopicus* across different Bird Conservation Regions (BCRs). BCRs are numbered roughly from northwest (BCR2 = western Alaska) towards the southeast (BCR60 = Sierra Madre de Chiapas).

$(F(2,55) = 98.99, P << 0.005)$ while remaining indistinguishable for the southern group $(F(2,24) = 1.58, P = 0.23)$.

7.5 Discussion

Implications of differential morphological selection within North American *Picoides* sensu lato, *L. villosus* varies significantly with respect to latitude, and is similarly correlated to temperature. The results indicate that variation in *L. villosus* body mass is an adaptation to climate, and that *L. villosus* is not morphologically constrained within a specific Grinnellian niche. Indeed, *L. villosus* populations vary in their foraging ecology and morphology across their distribution, with two major genetic clades occurring in North America [204]. The south and west clade displays greater amounts of genetic variation than its north and east counterpart, with ecological niche reconstructions indicating greater stability through time for the south and west populations [204]. Both clades demonstrate variation in foraging style based on regional abiotic and biotic factors [182]. *Leuconotopicus villosus*' mimic, *Dryobates pubescens*, stands in contrast, with much smaller magnitude responses to environmental factors. While variances in size (using other variables as proxies) are well documented within *D. pubescens* [183], the magnitude of these trends is shallow compared to *L. villosus*. At present, there is no published phylogeographic analysis for *D. pubescens* to compare to the structure observed in *L. villosus*. *Dryobates pubescens* shows greater consistency in foraging ecology than *L. villosus* throughout its distribution, preferentially foraging on small limbs, weeds, and branches [181]. The apparently constrained variation in *D. pubescens* contrasts with the major trends observed in *L. villosus*; this contrast is maintained in the foraging literature, where the foraging styles of *L. villosus* are more variable [181, 182, 203]. The plasticity of *L. villosus* with respect to foraging, phenotype, and morphology may be partially attributable to the different picid communities in which it occurs over its distribution, but more research is required.

Local responses to picid competition have been documented in *D. pubescens*, but these

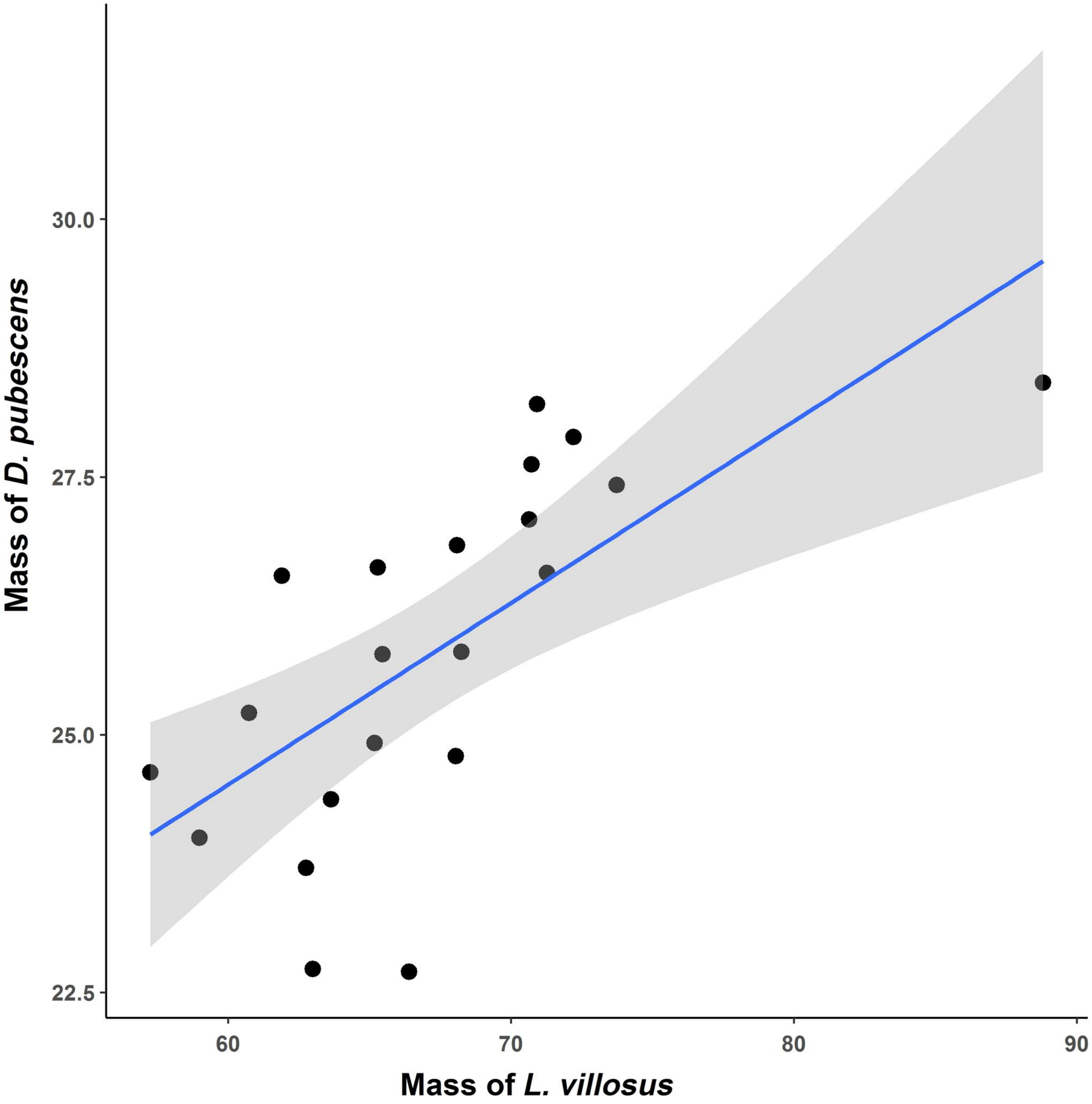

Figure 7.3: A regression of the mass of *Dryobates pubescens* and *Leuconotopicus villosus*. Each point represents the average of each species in a particular Bird Conservation Region (BCR); thus, the graph shows the relation in body size between *D. pubescens* and *L. villosus* by geographic area. The equation for the line is $y = (0.18 \pm 0.08)x + (13.93 \pm 5.88)$ with an adjusted $R^2 = 0.46$.

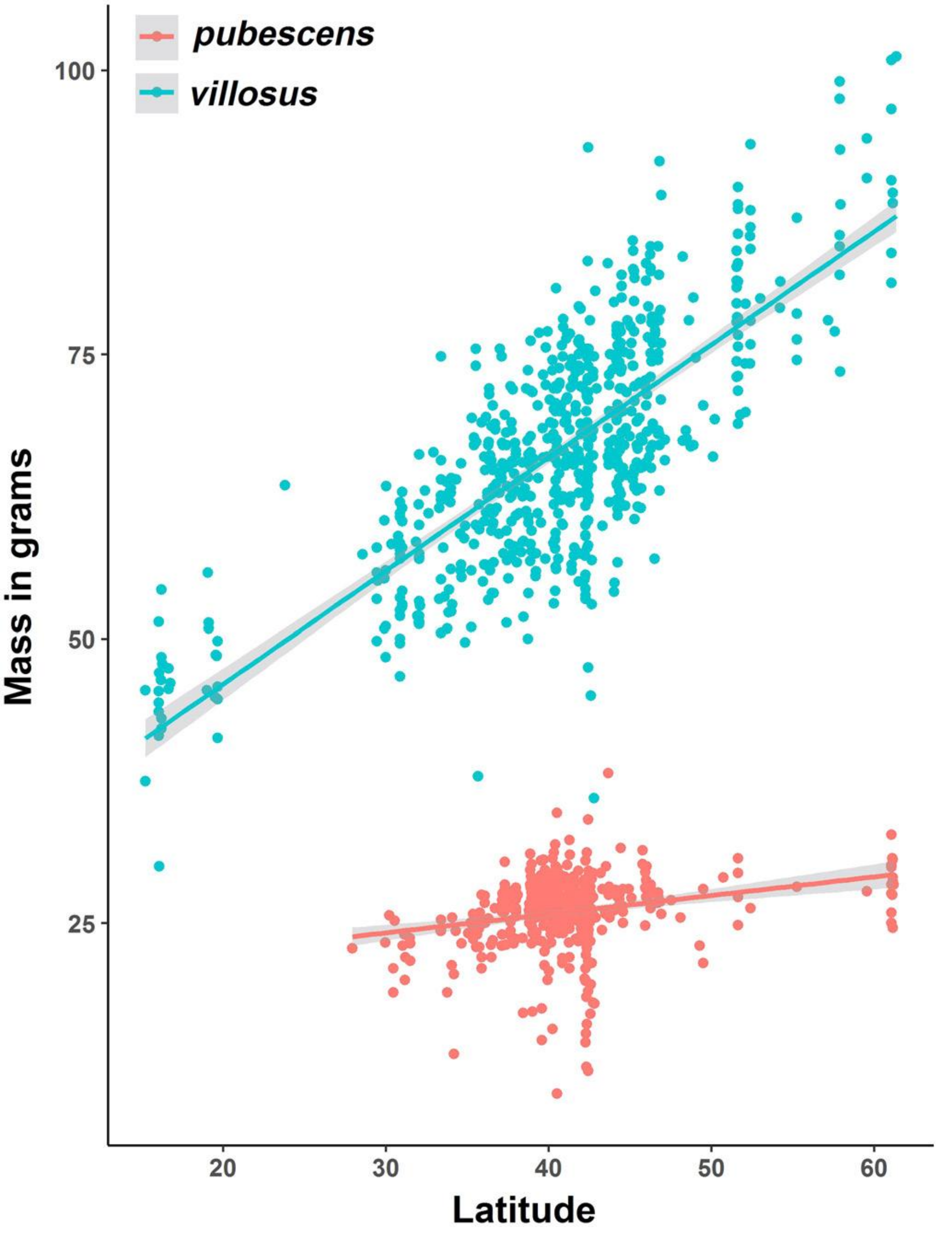

Figure 7.4: Relationship of mass to latitude for *Dryobates pubescens* and *Leuconotopicus villosus*. The equations for the lines are as follows: *D. pubescens* $= (0.16 \pm 0.06)x + (19.23 \pm 2.40)$, adjusted $R^2 = 0.07$; *L. villosus* $= (1.00 \pm 0.06)x +$ (26.11 ± 2.64), adjusted $R^2 = 0.58$.

responses appear to be related to direct access to resources and less related to foraging plasticity [265, 371]. The social behaviors of *Dryobates pubescens* and *Leuconotopicus villosus* also diverge from the expectation within a mimicry-dominated system, with *L. villosus* acting more aggressively towards *D. pubescens* than would be expected under a strict ISDM hypothesis [210]. The lack of evidence for adhering to an ISDM dynamic and the lack of major size variation within *D. pubescens*' distribution suggests that it may occupy a more specific Grinnellian niche (with respect to foraging ecology) that causes a constraint in body size. While the overall size ratio between models and mimics may be beneficial to the formation of ISDM systems, the evolutionary pressure to maintain these systems is apparently not as strong as other ecological pressures on morphological evolution in *D. pubescens* and *L. villosus*.

Within the large Neotropical woodpeckers, *Dryocopus lineatus* as a whole showed little evidence for clines with respect to latitude or environment variation. Central and South American populations have greater masses than those found in northern Central and North America. *Dryoscopus lineatus* were significantly larger in areas where they overlap with a larger model taxon, a possible indication that *D. lineatus* is tracking the mass of its models. There were insufficient data to determine if the trending of a 67–80% size of mimic to model was maintained throughout the Neotropics (in contrast to the 55–60% ± 3.8% by Prum [278]), but the size of *D. lineatus* is correlated with larger *Campephilus* at a local scale (*i.e.* within each *Campephilus*' individual distribution). This is especially apparent in North and Central America, where there appears to be a significant trending towards larger body size as one moves south. *Dryocopus lineatus* demonstrates an apparent lack of body size change in the southern portion of its distribution, but this is potentially clouded by a lack data for regional analyses with other *Campephilus* woodpeckers. The southernmost populations of *D. lineatus* occur outside of the distribution of *C. melanoleucos*, and are sympatric with *C. robustus* and *Celeus galeatus*, where they may be subject to a different selection regime for size. Both northern and southern populations of *D. lineatus* assessed in this study are ca one standard deviation above the average size ratio reported by Prum [278], bringing into question how consistent size differences must be to indicate ISDM systems.

7.5.1 Notes on ecogeographic trends

Previous studies have recovered a similar trend for size gradation across latitude and environment in Nearctic woodpeckers, with these trends being attributed (at least in part) to Bergmann's rule (*i.e.* the trending of species to have larger body masses in colder climates [28, 183]. Despite this, more expansive studies of tropical and Nearctic taxa have failed to show universality of Bergmann's rule, suggesting that more than environment is affecting the size of some taxa [117, 381]. One hypothesis is that these changes are more closely related to a taxon's foraging according to the Grinnellian niche [381] or to the Eltonian niche [239]. Zink and Remsen [381] discuss this with birds specifically, noting that ecological factors other than temperature may lead to species possessing larger ranges at high latitudes, thereby mirroring the effects of temperatures. For example, Nearctic woodpeckers may possess larger territories in the north because food is less plentiful at some times of year; larger birds may be better adapted for foraging across these larger territories [185]. Misinterpretation of these correlations may occur with some work on Bergmann's rule in North America, where wing length has been used as a proxy for overall bird size despite these characters not necessarily being linked [183, 381]. Furthermore, other work has shown that taxa may exhibit an ecological release at higher latitudes not just as a response to environment, but as a response to community structure. McNab [239] discussed several mammalian predators that exhibit larger sizes in different geographical regions, but that these trends are sometimes restricted to areas in which related dominant taxa do not occur. The effects of community composition and food availability on species size should be further investigated in birds, especially in species that have broad latitudinal ranges (*e.g. Leuconotopicus villosus*).

I have corrected for a potential ecological release affecting body size (as noted by McNab [239]) by selecting a complex in which one mimic is nearly entirely syntopic with one

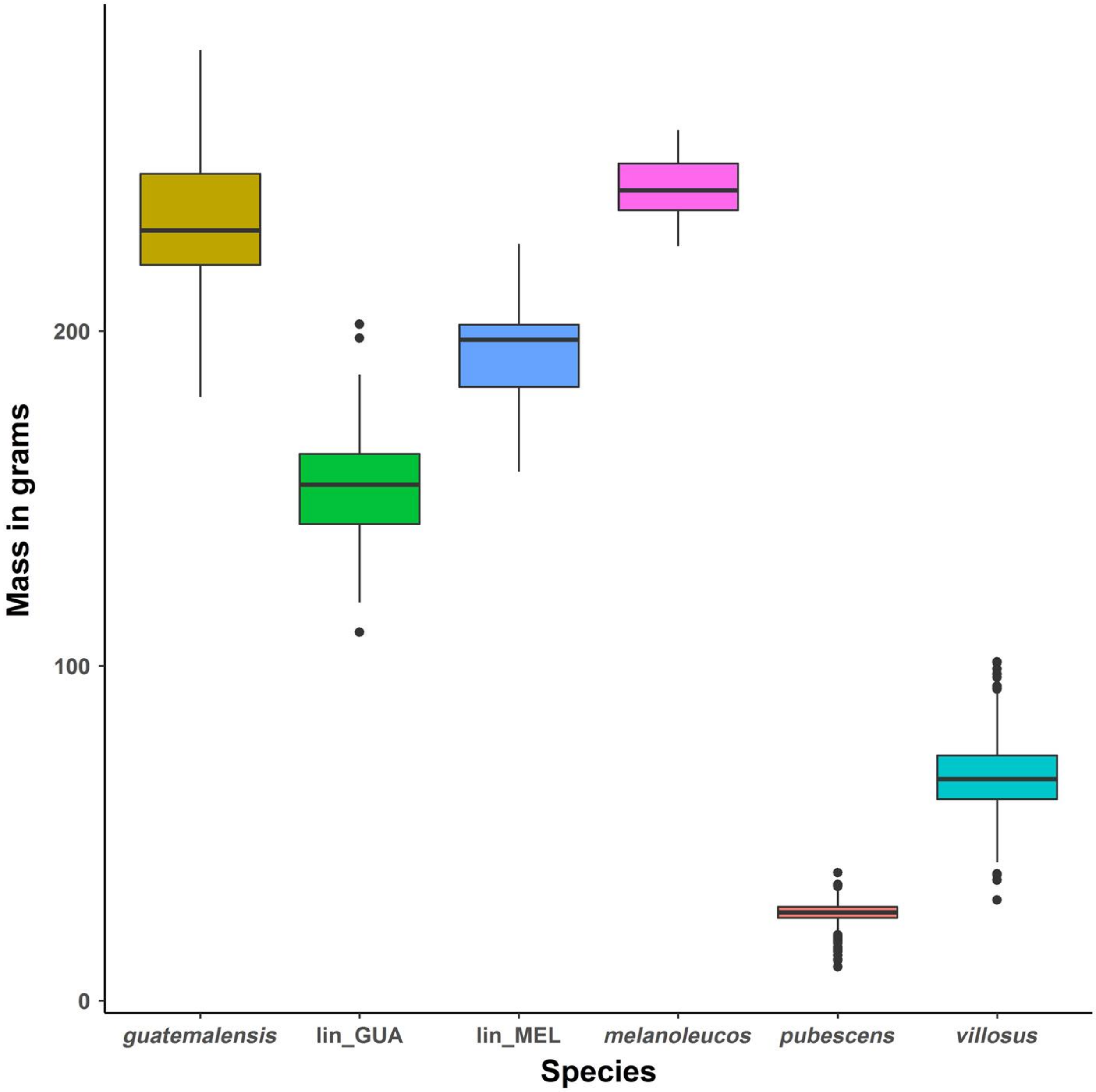

Figure 7.5: Mass comparisons of *Campephilus guatemalensis*, *C. melanoleucos*, *Dryocopus lineatus*, *Dryobates pubescens*, and *Leuconotopicus villosus*. The annotations of 'lin-GUA' and 'lin-MEL' correspond to populations of *D. lineatus* that are sympatric with *C. guatemalensis* and *C. melanoleucos*, respectively.

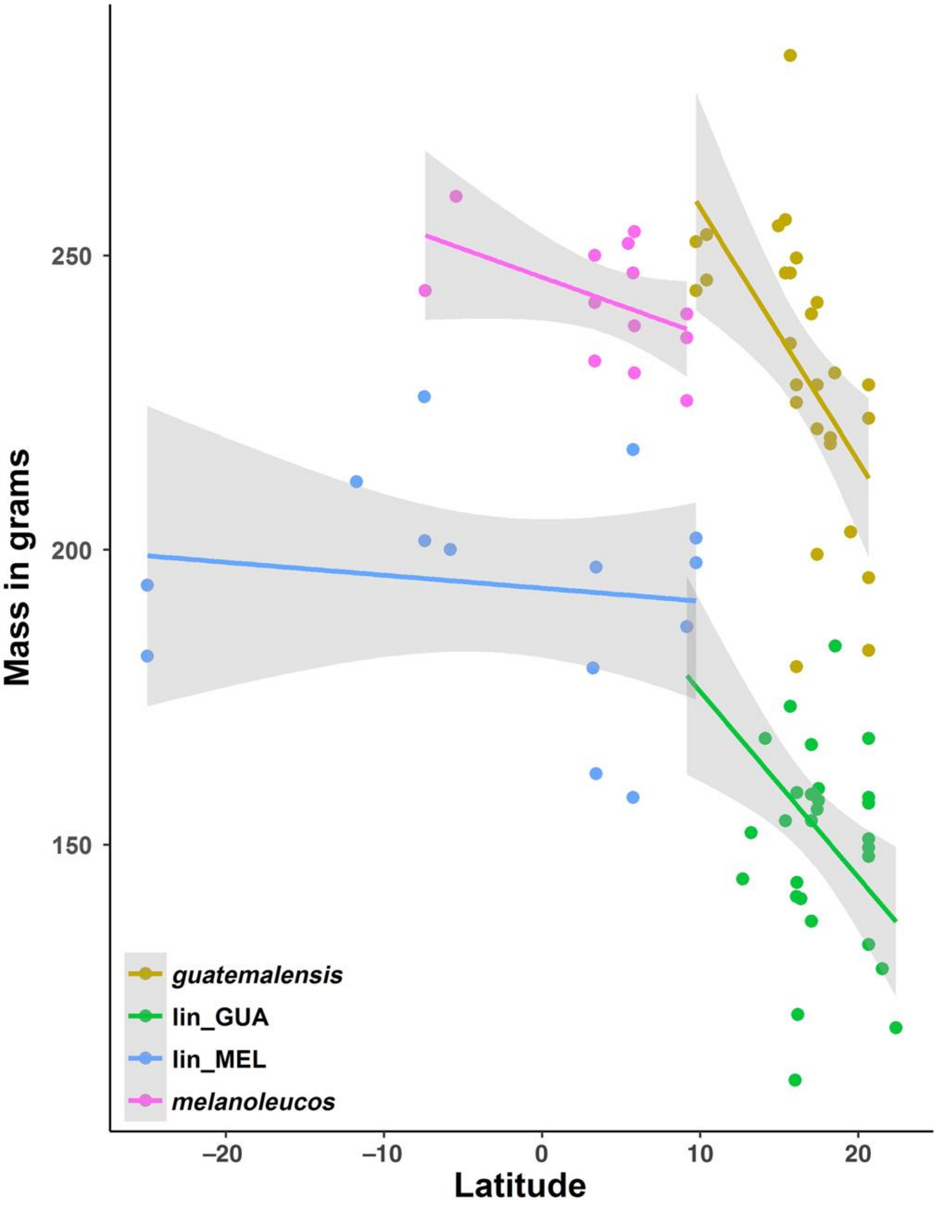

Figure 7.6: Linear regressions of mass to latitude for *Campephilus guatemalensis*, *C. melanoleucos*, and *Dryocopus lineatus*. All taxa possess larger birds in the southern parts of their distribution. Equations for the regressions are as follows: *Campephilus guatemalensis* = $(-4.30 \pm 2.46)x + (301.08 \pm 41.04)$, adjusted $R^2 = 0.33$; *C. melanoleucos* = $(-0.96 \pm 1.04)x + (246.29 \pm 6.70)$, adjusted $R^2 = 0.24$; *D. lineatus* (northern or '**lin-GUA**') = $(-3.16 \pm 1.94)x + (207.60 \pm 33.40)$, adjusted $R^2 = 0.27$; *D. lineatus* (southern or '**lin-MEL**') = $(-0.22 \pm 0.92)x + (193.48 \pm 10.74)$, adjusted $R^2 = 0.02$.

model taxon, and it appears that the trending towards Bergmann's rule demonstrated by *Dryobates* and *Leuconotopicus* is a response to multiple environmental and ecological conditions. Confirming the findings of Zink and Remsen [381], I found that temperature and environmental variation do not explain variability as well as latitude, thus implying that other factors (*e.g.* day length, seasonal food productivity) not included in environmental data may be affecting woodpeckers' masses. For the Neotropical taxa, it appears that ecological selection will outweigh purely environmental selection for body mass in the widespread *D. lineatus* in the northern hemisphere, thus resulting in the latitudinal trends paralleling sympatric *Campephilus* presented herein (Fig. 7.6). Furthermore, while longitudinal trends could exist with respect to mass (mirroring trends observed in phenotype in North America attributed to Gloger's rule, *i.e.* that darker and more pigmented populations occur in more humid environments [134, 303]), I failed to recover any strong trends. Analyses of such trends can be confounded by the geography of the Americas, wherein many ecoregions (*e.g.* BCR 4: the Northwestern Interior Forest) exist without similar habitats to their south and many habitats are distributed in north-south bands (*e.g.* BCR18: the shortgrass prairie [32]). This can cause a covariation of longitudinal trends with latitudinal and environmental trends within analyses. Finer scale sampling is needed to allow for the analysis of species within latitudinal transects to correct for this covariation.

7.5.2 Expansion of research

Trends such as Bergmann's rule are often related to firm responses to environment (*i.e.* Hutchinsonian niches), and have less often been examined in relation to other ecological niche definitions. Examining a species' foraging ecology and community interactions in tandem with environmental and latitudinal trends sheds light on a species' ecological evolution on multiple scales. This research has demonstrated character disjunction within complexes of organisms with Eltonian dynamics, and reinforces that ecological selection driven by a taxon's community and specific ecology may be differentially affecting aspects of a taxon's morphology and phenotype. It is possible that the macroevolutionary scaling of mimicry presented by Prum [278] is true across broad spatial areas, and that this trend is an example of the Eltonian noise hypothesis in that fine-scale relationships are clouded by the macro-scale analyses [324]. Larger comparative analyses of size in purported ISDM systems in specific regions will reveal whether other species are 'locked' into specific morphospaces to mimic dominant sympatric taxa or if such ratios only exist when species are examined across their entire co-distribution. If the ratio holds true only at coarse scales, then it is possible that certain size ratios are more amenable to the development of mimicry even if this ratio does not have to be strictly maintained through time or across geographic space to perpetuate the mimicry dynamic. Parallel analyses should compare pairs of taxa with similar phylogenetic and ecological relatedness that co-occur broadly and do not share similar phenotypes to provide a null comparison of sympatric ecogeographic variation in systems lacking mimicry. If results are similar to those found in mimicry systems, then communities' ecomorphological evolution as a whole are likely being driven by other abiotic and biotic factors [123].

Future work with ecogeographic clines should focus on multi-character assessments that take into account aspects of functional morphology (*e.g.* bill length) as well as gross mass, phenotype, and community interactions. Fine scale data,such as those that are available from consistent local collecting and banding operations, will permit analyses of microhabitat evolution and insights into how different community members respond to environmental changes [183]. Combining these data with known interspecific interactions will provide an idea of how a species' habitat and community are affecting its ecological niche and, therefore, its evolutionary trajectory. While phenotype was not quantified in this study, there are five presently recognized subspecies of *Dryocopus lineatus*, many of which possess plumage characteristics paralleling sympatric *Campephilus* species [130, 167]. Perhaps the most striking example of this local adaptation is in western South America, where the notably browner subspecies *D. lineatus fuscipennis* co-occurs with the distinctively brownish *Campephilus guayaquilensis* [299]. No population level genetic analysis of *D. lineatus* exists, so it is unknown to what extent these geographic phenogroups interbreed or experience selection to maintain their local *Campephilus*-like phenotype. Bioacoustics also were not included in this study, but are an important aspect of proposed ISDM systems. Visual signaling is integral to ISDM theory and is undoubtedly occurring in wild picids, but birds also must be detecting each other acoustically as well [278]. Many non-ISDM species are known to mimic the vocalizations of potential competitors or predators, while other species have apparently converged on similar vocalizations by means of natural selection [196]. Vocal convergence should be quantified in ISDM systems as well to understand to what extent mimics diverge from their close relative and converge on their presumed models (M. B. Robbins and Anon. reviewer pers. comm.).

Ecological niche research, thus far, has focused on factors determining overall distribution and macro-scale patterns of interaction with other species, mainly through competition. Less research has focused on the finer-scales of niche evolution dynamics, be it local niche conservatism or niche differentiation across geographic space within a single clade or taxon [165]. Recent papers have focused on quantifying differences between species ecological niches on the whole to determine if species are diverging [135, 237, 358], with the consensus now being that niches are generally conserved through time [267, 269, 270] but that secondary contact can encourage character divergence in sympatry [184, 202]. Regiospecific studies of widespread, polytypic species (such as *Dryobates pubescens*, *Dryocopus lineatus*, and *Leuconotopicus villosus*) incorporating morphological and genetic data will provide an opportunity for understanding if ecogeographic variation is truly conservative, Brownian (*i.e.* stochastic and random) in nature, or the result of highly selected regional niche evolution in response specific community and environmental factors [165, 204].

7.6 Conclusions

Studies of ISDM are limited, and likely do not reflect the full extent of the phenomenon either within the class Aves or beyond. This form of mimicry is complex in that it can evolve in a two-observer system and does not necessarily require a third party observer to cause evolutionary pressure within the system. As I have shown here, mimics do maintain smaller sizes than their models, but what size is necessary for effective mimicry is still undetermined. In the Neotropics, a parallel ecogeographic relationship in size between *Dryocopus lineatus* and overlapping species of *Campephilus* exists, suggesting that community members influence each others' physical traits (and, therefore, morphological evolution via their Eltonian niches). Observed trends within this group seem to counter Bergmann's rule, at least in the case of *Campephilus guatemalensis* and *Dryocopus lineatus*, for reasons that are unknown. Conversely, Nearctic taxa follow Bergmann's rule but differ significantly in their responses to abiotic factors, demonstrating that mimics and models can possess correlated phenotypic evolution contemporaneously with disjointed morphological evolution. This comparison of sympatric Nearctic taxa shows that while similar environmental trends in body mass can exist concurrently for mimics and models, the magnitude of their responses may be a reflection of the relative importance of selection with respect to abiotic factors, their communities, and/or their foraging regimes. While mass ratios differed from the ISDM expectation in a pair of Neotropic woodpeckers, the trending towards larger mimics in areas with larger models also holds true, and highlights the need for more research on Eltonian dynamics.

7.7 Acknowledgments

I would like to thank J. Bates, N. Cordeiro, J. Engel, J. T. Wootton, and three anonymous reviewers for critical comments both on the theory presented here and the manuscript itself. I also thank J. Soberón for discussions concerning Eltonian niche theory, and F. Bienvenu for discussions regarding statistical methods.

7.8 Funding

This work was funded by my graduate program, the Committee on Evolutionary Biology at the University of Chicago.

7.9 Ethics statement

This work is based entirely upon data freely available online. Code and information derived from this study is likewise available for future use.

7.10 Disclaimer

This chapter is available as a peer-reviewed publication via the *Journal of Avian Biology* [69]. This chapter has been adapted for the sole purposes of meeting the requirements of a University of Chicago PhD. Some program packages cited herein are cited as more recent versions, but versions quoted in text were used in the analyses detailed herein.

CHAPTER 8

CONCLUSIONS & FUTURE RESEARCH

8.1 Overview

Throughout this manuscript, I have demonstrated the ways in which biogeography and ecology influence and shape avian diversification across various spatiotemporal scales. Using phylogenies of birds and mammals and my own theoretical analyses, I have clarified how extinction dynamics build diversity in tropical systems. Using case studies from the Afromontane mountains, I have illustrated and clarified connectivity between different montane systems in the modern era while simultaneously providing case studies for individual species on the mode and method of diversification across ecological gradients and across biogeographic barriers. Lastly, I have illustrated how ecological interactions can constrain morphological variation within taxa, and how ecological gradients can likewise lead to morphological diversification and parapatric diversification within taxa.

This dissertation is the result of five years of work at the University of Chicago and the Field Museum, and builds strongly upon three years of work at the University of Kansas and with the Biodiversity Initiative as well as four years of undergraduate work and research exposure at Louisiana State University. My experiences and my mentors have helped me to analyze the natural world around me critically and in novel ways, while at the same time learning how to re-apply and extend previous research in light of new data and new ideas.

8.2 Advances to the field

This work extends previous research by applying rigorous and novel techniques to historical problems of biogeography and ecology. My work in Africa rigorously examines regional biogeography using a wide range of methods designed to provide in-depth analyses of regional relationships. Combined with information about individual species distributions and theoretical tests of speciation dynamics, I am able to demonstrate the differential effects of biogeographic barriers, the differential responses of species across the same biogeographic barriers, and the effects of regional extinction on the creation and maintenance of Afrotropical species communities.

Furthermore, combining these data with ecological niche models and ecological analyses provides novel perspectives on regional evolution and diversification in birds, especially with regards to ecological gradients in Central Africa and across gradients in which species are 'locked' into mimicry dynamics. This work helps illustrate the interplay between ecological diversification and ecological evolution and biogeography, and sets the stage for future studies on these factors.

8.3 Continued research

As I write this, I am working with Kellie McKague (Field Museum), Taylor Hains (University of Chicago & Field Museum), J. Dylan Maddox (Field Museum, American Public University System, & Universidad Científica del Perú), John M. Bates (Field Museum), Ben D. Marks (Field Museum), and Joseph D. Manthey (Texas Tech University) to perform further sequencing of birds in the Afromontane region, specifically of birds from the Lacustrine Rift and from within the Cameroon highlands. This work, while delayed on account of COVID-19, is still moving forward and will shed more light on the dynamics within montane areas. Furthermore, I will be working with my future colleagues at the University of Kansas and elsewhere to continue analysing and studying the ways in which ecological gradients drive species evolution and community dynamics.

8.4 Future studies

There are many questions about the diversification of birds that remain unanswered, and in many ways this dissertation is merely a stepping stone towards a better understanding of these systems. Sorely lacking is an in-depth analysis of species across the Afromontane landscape to understand connectivity and species relationships. These studies are needed to understand the concordance dissonance between different species dynamics in order to understand if colonization patterns in montane landscapes are truly random or if certain patterns predominate among specific guilds or clades of birds [72, 349].

Research should also focus on the ways in which ecological gradients drive parapatric diversification, particularly within montane regions. Many species of Central Africa bird experience diversification across elevational gradients in spite of gene flow (*e.g.*, *Chloropicus ellioti*) [31, 72, 306] and these gradients appear to be maintained and static in spite of ongoing gene flow in specific hybrid zones, despite these populations being grouped together based on strict adherence to the biological species concept [306, 307]. Furthermore, the Cameroonian highlands feature a strange pattern of elevational replacement between adjacent lowland taxa, where members of the same communities (from Central Africa) are repeatedly forced into higher elevations when co-occuring with their West African congeners [43, 99]. There are exceptions to this rule (*e.g.*, *Melignomon eisentrauti*) [43] and the adjacent island of Bioko appears to host both high elevation Central African taxa and near-relictual Central African taxa that do not necessarily occur on the adjacent coast of Cameroon (*e.g.*, *Ploceus nigricollis brachypterus*) [31, 263]. The ecological interplay of competitive exclusion and of niche occupancy can thus be explored both along elevations where competitors are not present (*e.g.*, on Bioko) and in larger communities where competitive exclusion likely occurs. These studies can likewise be contrasted with studies from more 'neutral', homogeneous localities, such as the Sahel or the Yucatán.

8.5 Note on taxonomy and species limits

The studies contained within this dissertation have helped highlight the need for complete geographic sampling within studies of avian species in order to understand the full picture of geographic dynamics. Too many studies exclude major subspecies or major geographic populations while providing ‘species level’ phylogenetic trees. Papers such as Chapter 5 emphasize the importance of all sampling known, described, and formerly described populations to fully understand evolutionary dynamics. Furthermore, Chapter 4 highlights the need for sampling across major biogeographic barriers for species that lack described geographic variation as well, given that many taxa can be extremely conserved in characters when diversifying allopatrically (*e.g.*, *Batis diops*, which contains a potentially unnamed species from Mt. Kabobo).

This dissertation furthermore illustrates and stresses the importance of using hybrid species concepts that take into account multiple lines of evidence. By not relying on a single strict definition of species limits, this dissertation is able to better capture the existing variation in avian communities and therefore provide more accurate estimates of the limits of species. This is crucial in the modern era, when conservation is becoming increasingly important and marginalized and overlooked populations are at risk of going extinct. Indeed, Chapter 5 highlights resurrects the Lazarus taxon *Cinnyris preussi genderuensis*, an historically overlooked population that may merit species status pending further scientific investigation.

8.6 Conclusions

This dissertation illustrates the dynamics of avian diversification across multiple different spatiotemporal scales, driving forward theory in biogeography more broadly while providing specific case studies within birds. This dissertation has already been published in part, with the rest of this dissertation to hopefully be published in the coming years. This work has thus contributed to the field in multiple ways, providing information and perspective for better understanding evolutionary dynamics in multiple different systems. It is my sincere hope that this work will continue to be relevant in the future, and just like the dissertations on birds from the past that inspired me [318], I hope that this work will itself inspire and assist future scientists in their quest to understand more about avian diversification.

APPENDIX A

SUPPLEMENTAL CODE: CLIMATIC REFUGIA AND REDUCED EXTINCTION CORRELATE WITH UNDERDISPERSION IN MAMMALS AND BIRDS IN AFRICA

Full codes are available upon request. A reduced workflow is shown here.

This is the supplementary material for the manuscript by JC Cooper, NMA Crouch, A Ferguson, and JM Bates. This document is presented as is and will need to be tailored for use on different machine and for different datasets. Much of this was run on **R** 3.6.3 on a Linux server at UChicago. Final analyses were run locally in **R** 4.0.4 on a Linux operating system [286].

```
library(ape)

library(colourvalues)

library(dismo)

library(ggpubr)

library(gridExtra)

library(maptools)

library(PhyloMeasures)

library(raster)

library(rasterVis)

library(rgdal)

library(rgeos)

library(sf)

library(sp)

library(tidyverse)

library(TreeSim)

library(viridis)
```

A.1 Diversity analyses

The following outlines the code required for analysing species diversity and phylogenetic diversity within out datset. Note that this code assumes the existence of the presence-absence matrices (PAMs) for birds and mammals.

A.1.1 Aggregating names

The following strips and saves names for subsequent analyses:

```
comm_coords=read_csv(paste0(filepath,"mammal_pam_coords.csv"))
mamm.dat=comm_coords%>%dplyr::select(-Var1,-Var2)
coords=comm_coords%>%dplyr::select(Var1,Var2)

bird.dat=read_csv(paste0(filepath,"fixed_birds_pam.csv"))

write_csv(coords,paste0(filepath,"raster_coords.csv"))

names=colnames(mamm.dat)

write_csv(as.data.frame(names),paste0(filepath,"download_names.csv"))
```

A.1.2 Calculating metrics

Species diversity

We can calculate richness (α diversity) by calculating the row sums, and then compare them.

```
spdv.mamm<-rowSums(mamm.dat)
spdv.bird<-rowSums(bird.dat)


# visualize with gghistogram
```

```
a=gghistogram(spdv.mamm,add="mean",
        rug=F,#add_density=T,
        bins=250) +
        xlab("Species Diversity")+
        labs(title="Mammal Richness")+
        scale_y_continuous(limits=c(0,11000))

b=gghistogram(spdv.bird,add="mean",
        rug=F,#add_density=T,
        bins=250) +
xlab("Species Diversity")+
labs(title="Bird Richness")+
scale_y_continuous(limits=c(0,11000))
```

Outputs at all steps were normalized using the equation $\frac{x' - min(x')}{max(x') - min(x')}$. This changed every vector to being between 0 and 1.

```
# normalize values

normalize=function(x){
        max=max(x)
        min=min(x)
        out=(x-min)/(max-min)
        return(out)
}
```

Random rasters were also created for comparisons and likewise normalized, using the following custom function.

```
randomize==function(df,seed){
        #set.seed(81507)
```

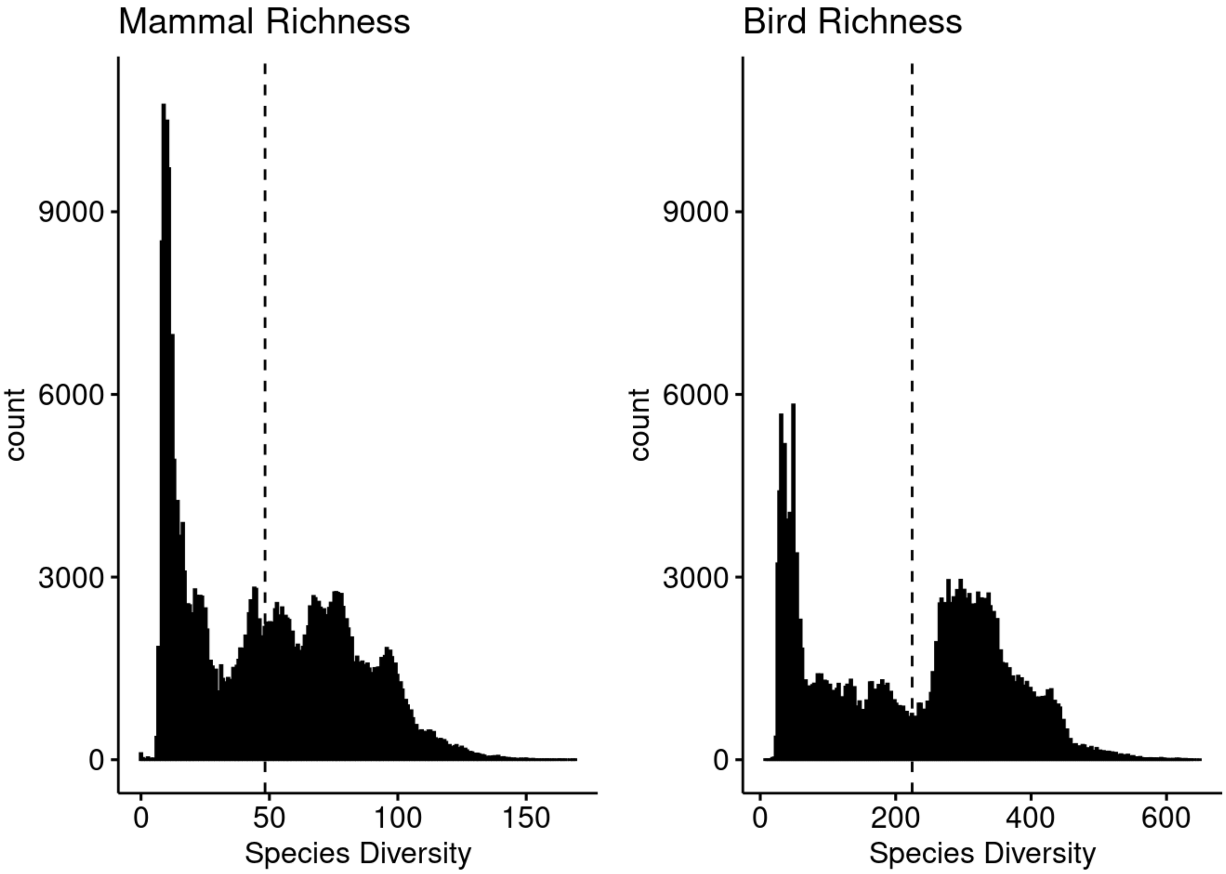

Figure A.1: Histograms of species diversity for birds and mammals. Note that the overall shape of the profiles is similar, while the overall counts per cell vary greatly given the larger number of bird species.

```
        set.seed(seed)
        df.x=df[,3]
        for(i in 1:100){
                rando=sample(df.x)
                df[,(i+3)]=rando
        }

        cols.x=paste0(rep('random.',100),1:100)
        colnmes(df)[-c(1:3)]=cols.x

        return(df)
}

spdv.mamm.random=randomize(spdv.mamm.stand,81507)
spdv.bird.random=randomize(spdv.bird.stand,62901)

spdv.mamm.rast=rasterFromXYZ(spdv.mamm.random)
spdv.bird.rast=rasterFromXYZ(spdv.bird.random)
```

Similarities were then calculated using the real rasters and the random rasters.

```
# metric is "I" or "D"
# stack always has [[1]] as the 'real' layer, 2-101 random
# category is metric being compared
pare=function(stack1,stack2,metric,category){
mamm.stats=NULL
bird.stats=NULL
real.mamm=spdv.mamm.rast[[1]]
real.bird=spdv.bird.rast[[1]]
```

```
# Raster similarity

# similar to niche comparison tests
# need to test the difference of each to random rasters
# need to compare distributions to the 'real' difference

for(i in 2:101){
        # get randomized rasters
        r1=spdv.mamm.rast[[i]]
        r2=spdv.bird.rast[[i]]
        # perform comparisons
        # compare mamm to bird random
        mamm.stats[i-1]=nicheOverlap(real.mamm,r2,stat=metric)
        # compare bird to mamm random
        bird.stats[i-1]=nicheOverlap(real.bird,r1,stat=metric)
}

test.stat=nicheOverlap(real.mamm,real.bird,stat=metric)

print(paste0("Test: Mammals vs. Random Birds: ",category))
print(t.test(x=mamm.stats,mu=test.stat,alternative="two.sided"))
print(paste0("Test: ",test.stat))

print(paste0("Test: Birds vs. Random Mammals",category))
print(t.test(x=mamm.stats,mu=test.stat,alternative="two.sided"))
print(paste0("Test: ",test.stat))

print("Visualization:")
```

```
df.x=c(mamm.stats,bird.stats)
labs.x=c(rep("mammals",100),rep("birds",100))

df.x=as.data.frame(cbind(labs.x,df.x))
colnames(df.x)=c("Group","Value")

df.x$Value=as.numeric(df.x$Value)
df.x$Group=as.factor(df.x$Group)

a=ggplot(data=df.x,aes(x=Value,fill=Group))
b=scale_x_continuous(limits=c(0.5,1))
b.5=geom_density(alpha=0.6)
c=theme_classic()
d=geom_vline(xintercept=test.stat,colour="black",linetype="dashed")

print(a+b+b.5+c+d)
}

# example run
raster.compare(stack1=spdv.mamm.rast,
        stack2=spdv.bird.rast,
        metric="I",category="Richness")
```

A.2 Note on other metrics

Similar codes to those used above were used to obtain metrics from other variables.

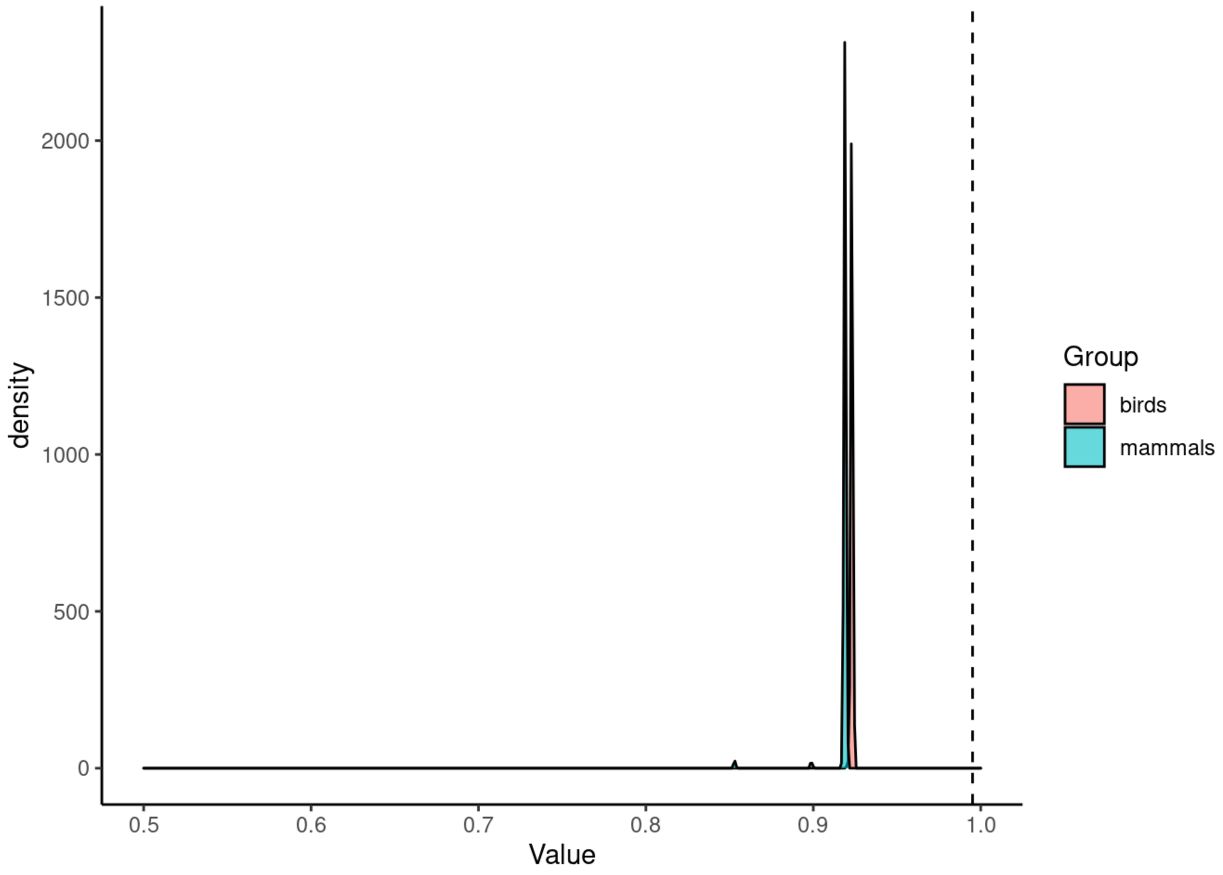

Figure A.2: Histograms of species diversity for birds and mammals. Note that the overall shape of the profiles is similar, while the overall counts per cell vary greatly given the larger number of bird species.

A.3 Theoretical analyses

Here, we perform our theoretical models of phylogenetic metrics with respect to identical communities that differ only in their extinction rates. We first define a function, disperse.sim, that is capable of creating random trees with a specified variable set. For all models, we hold constant low levels of speciation and extinction, and define the variable extinction via mass extinction events that are always more severe for areas that lack refugia.

```
# function for creating trees with
# specific species pools and extinction rates


disperse.sim=function(n, # number of taxa in a community
                numbsim, # number of simulations to perform
                lambda, # vector of speciation rates
                mu, # vector of extinction rates
                frac, # fraction survival (mass extinctions)
                times){ # times at which events occur


        out.sim=sim.rateshift.taxa(n=n,
                numbsim=numbsim,
                lambda=lambda,
                mu=mu,
                frac=frac,
                times=times,
                complete=F) # extinct species not returned


        mntd=NULL
        mpd=NULL


        for(i in 1:numbsim){
```

```
                tips=out.sim[[i]]$tip.label

                # create matrix for performing tests
                tip.vals=rep(1,length(tips))
                tip.mat=t(as.matrix(tip.vals))
                colnames(tip.mat)=tips

                mpd[i]=mpd.query(out.sim[[i]],
                        tip.mat,
                        standardize=F)
                        # don't standardize
                        # keep comparable
                mntd[i]=mntd.query(out.sim[[i]],
                        tip.mat,
                        standardize=F)
        }
        out.mat=cbind(mpd,mntd)
        return(as.data.frame(out.mat))
}

# histogram plotting function

plot.hist=function(x.stable,y.unstable,val){
        x=cbind("Stable",x.stable)
        y=cbind("Unstable",y.unstable)
        colnames(x)[1]=colnames(y)[1]="State"

        xy=rbind(x,y)
        cols=viridis(2)
```

```
        p.x=gghistogram(xy,x=val,add="mean",rug=F,
        color="State",fill="State",
        palette=cols,bins=30)
        print(p.x)
}
```

A.3.1 Example run

The following is an example showing how parameters were applied to the above codes.

```
# define parameters

numbsim=200
n.suit=100 # community size
# unsuitable habitat community size
n.unsuit=n.suit/10
# % survival during mass extinction
frac.unstab=c(0.9,
        0.9,
        1)
# mass extinction with refugia
frac.stab=1-((1-frac.unstab)/10)
# constant low extinction rates
mu=rep(0.1,3)
# constant speciation rates
lambda=rep(1.75,3)
# define times across simulation
times=c(0,0.33,0.66)

### Example
```

```
suitable.stable=disperse.sim(n = n.suit,
        numbsim = numbsim,
        lambda = lambda,mu = mu,
        frac = frac.stab,
        times = times)

# NOTE other runs not shown here

# plot comparison

plot.hist(x.stable = suitable.stable,
        y.unstable = suitable.unstable,
        val = "mpd")
```

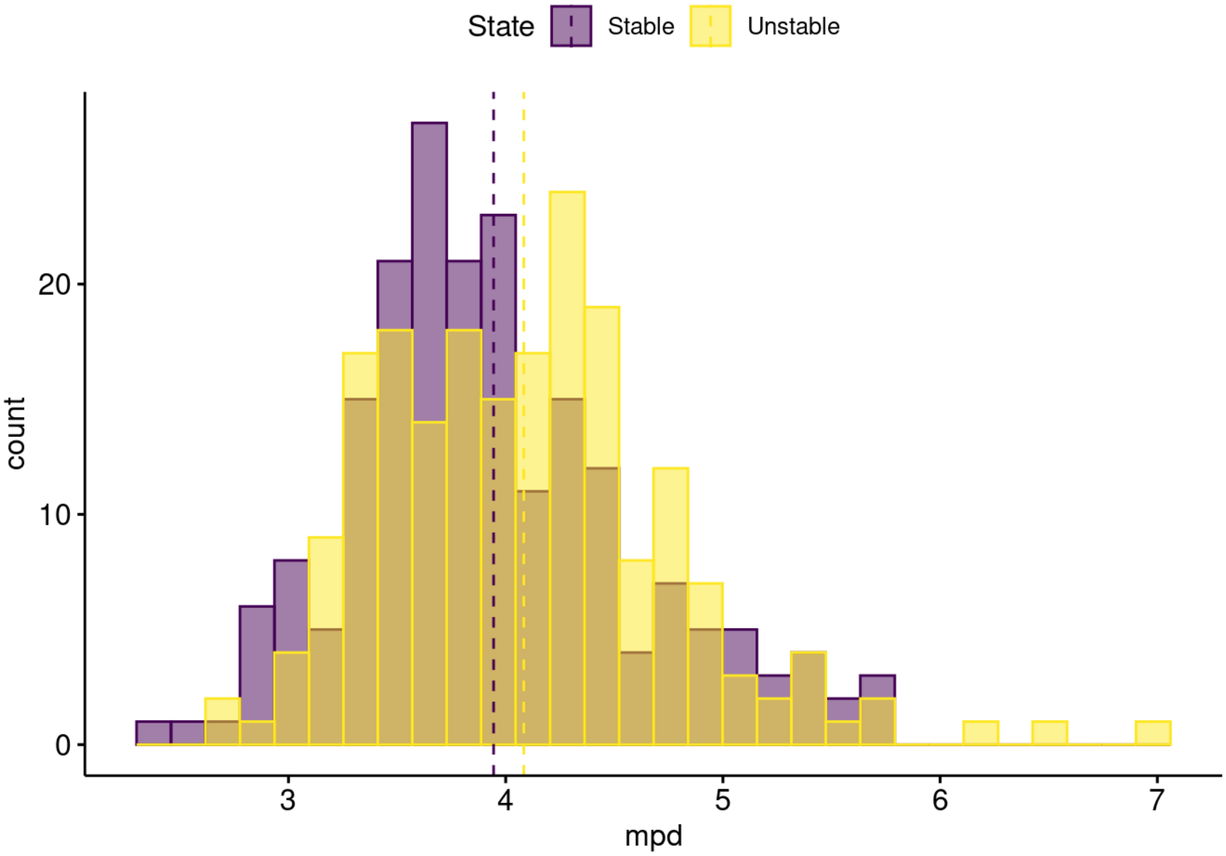

Figure A.3: Comparisons between the MPD values for stable and unstable conditions for an example set of runs. Means are shown with dotted lines.

APPENDIX B

HIERARCHICAL ANALYSES OF AVIAN COMMUNITY BIOGEOGRAPHY IN THE AFROMONTANE HIGHLANDS

Additional tables for this chapter can be found in the following pages.

Table B.1: Presence-absence matrix (PAM) of all species used in this study, with annotations for inclusion source (*e.g.*, Dowsett [93]) and inclusion in statistical analyses. Preview of B.1here; full table available via GitHub: `https://github.com/jacobccooper/dissertation_appendices`.

Bowie	**Dowsett**	**Exclude**	**Clements**	**Genus**	**Superspecies**	**Species**	**Group**	**Subspecies**
			24 583	*Zosterops*	*abyssinicus*	*abyssinicus*	*abyssinicus*	*abyssinicus*
		Exclude	24 584	*Zosterops*	*abyssinicus*	*abyssinicus*	*abyssinicus*	*arabs*
			24 585	*Zosterops*	*abyssinicus*	*abyssinicus*	*abyssinicus*	*omoensis*
			24 586	*Zosterops*	*abyssinicus*	*abyssinicus*	*socotranus*	*socotranus*
Yes	Yes		24 593	*Zosterops*	*poliogastrus*	*mbuluensis*	*mbuluensis*	*mbuluensis*
		Exclude	24 594	*Zosterops*	*abyssinicus*	*flavilateralis*	*flavilateralis*	*flavilateralis*
		Exclude	24 595	*Zosterops*	*abyssinicus*	*flavilateralis*	*flavilateralis*	*jubaensis*
Yes	Yes		24 607	*Zosterops*	*poliogastrus*	*silvanus*	*silvanus*	*silvanus*
Yes	Yes		24 609	*Zosterops*	*poliogastrus*	*winifredae*	*winifredae*	*winifredae*
Yes	Yes		24 615	*Zosterops*	*melanocephalus*	*melanocephalus*	*melanocephalus*	*melanocephalus*
			24 616	*Zosterops*	*brunneus*	*brunneus*	*brunneus*	*brunneus*
Yes	Yes		24 617	*Zosterops*	*poliogastrus*	*poliogastrus*	*kaffensis*	*kaffensis*
Yes	Yes		24 618	*Zosterops*	*poliogastrus*	*poliogastrus*	*kulalensis*	*kulalensis*
Yes	Yes		24 619	*Zosterops*	*poliogastrus*	*poliogastrus*	*poliogastrus*	*poliogastrus*
Yes	Yes		24 621	*Zosterops*	*poliogastrus*	*kikuyuensis*	*kikuyuensis*	*kikuyuensis*
Yes	Yes		24 622	*Zosterops*	*poliogastrus*	*eurycricotus*	*eurycricotus*	*eurycricotus*

Table B.2: Discrepancies between species lists used in this study. Column abbreviations are as follows: **B** = from Bowie [45]; **D** = from Dowsett [93], **New** = new taxa added in this study.

B	**D**	**New**	**Genus**	**Species**	**Notes**
Y			*Xenoperdix*	*udzungwensis*	Described after Dowsett [93] was published.
	Y		*Coturnix*	*coturnix*	Considered montane by Dowsett [93], but not by Bowie [45].
		Y	*Columba*	*oliviae*	Lower elevation, but highly associated with mountains in northern Somalia.
Y			*Columba*	*delegorguei*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Columba*	*albinucha*	Found in foothill and montane forest in Cameroon and the Lacustrine Rift.
	Y		*Streptopelia*	*hypopyrrha*	Considered montane by Dowsett [93], but not by Bowie [45].
Y			*Tauraco*	*livingstoni*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Tauraco*	*schalowi*	Excluded from analyses, but mentioned as it appears to associated with plateaus and other higher elevation (but not 'montane') habitats.
		Y	*Tauraco*	*corythaix*	Found in lower elevations in the south, but closely associated with mountains and found at higher elevations in the north.

Continued on following page.

Table B.2, continued.

B	D	New	Genus	Species	Notes
		Y	*Tauraco*	*erythrolophus*	Restricted to Angolan highlands; shows affinities with Tauraco bannermani.
Y			*Caprimulgus*	*solala*	Described after Dowsett [93] was published.
Y			*Caprimulgus*	*prigoginei*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Apus*	*aequatorialis*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Apus*	*melba*	Broadly distributed outside of Africa as well, but multiple endemic populations are found within Afromontane regions, illustrating regional patterns of connectivity.
Y			*Apus*	*aequatorialis*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Apus*	*aequatorialis*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Apus*	*niansae*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Apus*	*barbatus*	Ranges into adjacent lowlands in the south, but geographically associated with highlands and mountains, especially in the tropics.

Continued on following page.

Table B.2, continued.

B	D	New	Genus	Species	Notes
		Y	*Vanellus*	*melanopterus*	Breeds in highlands in tropical Africa, venturing lower in southern Africa and in non-breeding season; found near mountains throughout distribution, and shows associations with specific montane areas.
Y			*Bubo*	*vosseleri*	Mentioned in Dowsett [93], but at the time considered conspecific with Bubo poensis.
Y			*Glaucidium*	*albertinum*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Chloropicus*	*spodocephalus*	Recent split; considered conspecific with C. goertae and close to C. griseocephalus, the latter of which was considered montane by Bowie [45] and Dowsett [93].
		Y	*Platysteira*	*albifrons*	Also occurs in lowland, but wholly restricted to Angolan highlands.
		Y	*Platysteira*	*laticincta*	Restricted to montane forest in the Cameroon Line.
	Y		*Malaconotus*	*lagdeni*	Considered montane by Dowsett [93], but not by Bowie [45].
Y			*Terpsiphone*	*bedfordi*	Considered montane by Bowie [45], but not by Dowsett [93].
	Y		*Zavattariornis*	*stresemanni*	Considered montane by Dowsett [93], but not by Bowie [45].
Y			*Corvus*	*albicollis*	Considered montane by Bowie [45], but not by Dowsett [93].

Continued on following page.

Table B.2, continued.

B	D	New	Genus	Species	Notes
		Y	*Melaniparus*	*albiventris*	Found largely at mid to high elevations, and geographically confined to areas near montane regions.
Y			*Heteromirafra*	*archeri*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Calandrella*	*blanfordi*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Sphenoeacus*	*afer*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Macrosphenus*	*pulitzeri*	Foothills, but restricted to Angolan escarpment.
Y			*Macrosphenus*	*kretschmeri*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Eremomela*	*turneri*	Found in higher elevation (foothill) areas in Uganda and Kenya, in areas with other typically montane taxa (e.g., Kakamega). DRC population little known, at lower elevations, but occurs in Beni and one record from Uganda, suggesting it occurs at minimum in the region of the Western Rift.
		Y	*Schistolais*	*leontica*	Restricted to West African highlands.
		Y	*Apalis*	*binotata*	Associated with higher elevation areas, but also occurs at some lower elevation areas such as in Gabon (where other montane taxa, like Ploceus insignis, have been recorded).

Continued on following page.

Table B.2, continued.

B	D	New	Genus	Species	Notes
Y			*Apalis*	*personata*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Apalis*	*melanocephala*	Low elevation subspecies excluded, but many populations are restricted to montane habitats.
Y			*Apalis*	*karamojae*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Prinia*	*hypoxantha*	Restricted to montane escarpments in southern Africa. Formerly considered conspecific with P. maculosa.
Y			*Prinia*	*bairdii*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Eminia*	*lepida*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Cisticola*	*lugubris*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Cisticola*	*brunnescens*	Restricted mostly to montane habitats; occurs locally lower in e.g. Gabon, where other montane taxa also have been recorded at low elevations (e.g., Ploceus insignis).
		Y	*Schoenicola*	*brevirostris*	Found in many highlands, with some populations occurring lower in South Central Africa (where elevations are still relatively high). While range is relatively “broad”, displays same geographic patterns as other montane species.

Continued on following page.

Table B.2, continued.

B	**D**	**New**	**Genus**	**Species**	**Notes**
Y			*Bradypterus*	*baboecala*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Bradypterus*	*carpalis*	Associated with higher elevation wetlands, largely restricted to montane zones.
Y			*Locustella*	*alfredi*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Chlorocichla*	*laetissima*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Chlorocichla*	*prigoginei*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Phyllastrephus*	*lorenzi*	Restricted to foothills and mid-elevations in the Lacustrine Rift.
Y			*Phyllastrephus*	*poliocephalus*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Phyllastrephus*	*albigula*	Formerly considered conspecific with P. debilis. Restricted to montane regions.
Y			*Phylloscopus*	*laurae*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Phylloscopus*	*budongoensis*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Zosterops*	*abyssinicus*	Formerly considered conspecific with Z. flavilateralis; taxonomy of all East African White-eY recently assessed, with many new species being recognized.

Continued on following page.

Table B.2, continued.

B	**D**	**New**	**Genus**	**Species**	**Notes**
		Y	*Zosterops*	*flavilateralis*	Listed, but excluded; ventures into foothills, but found in lower elevations throughout.
		Y	*Zosterops*	*brunneus*	Only found at high elevations on Pico Basilé, similar to Z. melanocephalus.
		Y	*Illadopsis*	*rufipennis*	Noted for its affiliation with montane habitats in parts of the range, but excluded due to extensive low elevation populations.
Y			*Turdoides*	*hypoleuca*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Onychognathus*	*blythii*	Restricted to mountains along the northern Horn of Africa.
	Y		*Geokichla*	*guttata*	Considered montane by Dowsett [93], but not by Bowie [45].
		Y	*Geokichla*	*crossleyi*	Restricted to montane habitats.
		Y	*Muscicapa*	*adusta*	Largely restricted to montane regions in the tropics; throughout range, associated with higher elevations or montane regions. Not all populations included in analyses.
Y			*Melaenornis*	*fischeri*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Melaenornis*	*brunneus*	Considered montane by Bowie [45], but not by Dowsett [93].

Continued on following page.

Table B.2, continued.

B	D	New	Genus	Species	Notes
		Y	*Cossypha*	*polioptera*	Not wholly restricted to montane regions, but largely found in higher elevation regions across Africa.
Y			*Cossypha*	*dichroa*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Xenocopsychus*	*ansorgei*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Sheppardia*	*gunningi*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Sheppardia*	*gabela*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Monticola*	*rufocinereus*	Foothills and lower elevations, but strongly associated with montane regions.
		Y	*Monticola*	*rupestris*	Confined to mountainous regions along the southern Great Escarpment.
		Y	*Saxicola*	*torquatus*	Formerly considered conspecific with other Saxicola, namely S. rubicola. Some populations are low elevation, shows strong association with higher elevation moorlands and parklands throughout range.
Y			*Thamnolaea*	*cinnamomeiventris*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Oenanthe*	*bottae*	Considered montane by Bowie [45], but not by Dowsett [93].

Continued on following page.

Table B.2, continued.

B	D	New	Genus	Species	Notes
Y			*Oenanthe*	*dubia*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Oenanthe*	*lugubris*	Formerly conspecific with O. finschii. Highlands of East Africa.
Y			*Hedydipna*	*pallidigaster*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Nectarinia*	*bocagei*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Cinnyris*	*stuhlmanni*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Cinnyris*	*prigoginei*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Cinnyris*	*ludovicensis*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Cinnyris*	*habessinicus*	Occurs down to sea level, but clearly associated with wetter habitats and highlands as well; occurs almost to 2000 m.
Y			*Cinnyris*	*rufipennis*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Cinnyris*	*oustaleti*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Ploceus*	*spekei*	Mid-montane in most of range, but has some populations lower.
Y			*Ploceus*	*aureonucha*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Ploceus*	*nicolli*	Considered montane by Bowie [45], but not by Dowsett [93].

Continued on following page.

Table B.2, continued.

B	D	New	Genus	Species	Notes
		Y	*Euplectes*	*capensis*	Distribution parallels many other broadly Afromontane species; some populations lower but most populations restricted to highlands or areas adjacent to highlands.
	Y		*Euplectes*	*jacksoni*	Considered montane by Dowsett [93], but not by Bowie [45].
Y			*Nesocharis*	*ansorgei*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Estrilda*	*paludicola*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Estrilda*	*kandti*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Pytilia*	*lineata*	Considered montane by Bowie [45], but not by Dowsett [93].
		Y	*Motacilla*	*clara*	Distribution parallels many other broadly Afromontane species; some populations lower but most populations restricted to highlands or areas adjacent to highlands.
Y			*Anthus*	*cinnamomeus*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Anthus*	*hoeschi*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Anthus*	*similis*	Considered montane by Bowie [45], but not by Dowsett [93].

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Table B.2, continued.

B	**D**	**New**	**Genus**	**Species**	**Notes**
		Y	*Anthus*	*caffer*	Distribution parallels many other broadly Afromontane species; some populations lower but most populations restricted to highlands or areas adjacent to highlands.
		Y	*Rhynchostruthus*	*louisae*	Restricted to mountains in northern Somalia.
		Y	*Crithagra*	*xanthopygia*	Formerly considered conspecific with C. atrogularis and C. reichenowi.
Y			*Crithagra*	*flavigula*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Crithagra*	*xantholaema*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Crithagra*	*reichardi*	Considered montane by Bowie [45], but not by Dowsett [93].
Y			*Linaria*	*johannis*	Considered montane by Bowie [45], but not by Dowsett [93].

Table B.3: Species excluded from these analyses, with reason for exclusion.

Genus	**Species**	**Subspecies**	**Excluded Reason**
Columba	*larvata*	*principalis*	Príncipe; outside study area.
Columba	*larvata*	*simplex*	São Tomé; outside study area.
Tauraco	*livingstoni*		All subspecies excluded; T. l. cabanisi broadly distributed in East African lowlands.
Tauraco	*schalowi*		Semi-montane; broadly distributed in lower elevations of Zambia and adjacent regions.
Apus	*aequatorialis*	*furensis*	Darfur; region excluded from analyses.
Apus	*melba*	*melba*	European migrant.
Apus	*melba*	*tuneti*	North African and Asian migrant.
Apus	*melba*	*marjoriae*	Namibian highlands; region excluded from analyses.
Apus	*melba*	*willsi*	Madagascar; outside study area.
Apus	*melba*	*nubifugus*	Himalayas; outside study area.
Apus	*melba*	*dorabtatai*	India; outside study area.
Apus	*melba*	*bakeri*	Sri Lanka; outside study area.
Sarothrura	*ayresi*		Migrant with incompletely known distribution; Ethiopia south to South Africa.

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Table B.3, continued.

Genus	**Species**	**Subspecies**	**Excluded Reason**
Telophorus	*olivaceus*	*vitorum*	Mozambican lowlands.
Macrosphenus	*kretschmeri*	*griseiceps*	Local in eastern Tanzania and Mozambique outside study area.
Artisornis	*moreaui*	*sousae*	Njesi Plateau; region excluded from analyses.
Apalis	*jacksoni*	*minor*	Lowlands from Cameroon to Democratic Republic of the Congo.
Apalis	*chariessa*	*chariessa*	Lowlands in Kenya (possibly extinct).
Apalis	*melanocephala*	*melanocephala*	Lowlands from Somalia to Tanzania.
Eminia	*lepida*		Found in many higher elevation areas but not restricted to montane regions.
Cisticola	*ayresii*	*gabun*	Bateke Plateau region; region excluded from analyses.
Phylloscopus	*umbrovirens*	*yemenensis*	Yemen; outside study area.
Sylvia	*lugens*	*clara*	Matengo Highlands; region excluded from analyses.
Zosterops	*abyssinicus*	*arabs*	Arabian Peninsula; outside study area.
Illadopsis	*rufipennis*		Multiple subspecies; many are lowland. May need taxonomic revision for E vs. W Africa.
Geokichla	*piaggiae*	*rowei*	Nguruman Hills and adjacent N Tanzania; region excluded from analyses.

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Table B.3, continued.

Genus	**Species**	**Subspecies**	**Excluded Reason**
Muscicapa	*adusta*	*mesica*	Zimbabwean lowlands.
Cossypha	*caffra*	*namaquensis*	Namibia to South Africa; region excluded from analyses.
Pogonocichla	*stellata*	*macarthuri*	Chyulu Hills; region excluded from analyses.
Sheppardia	*gunningi*	*gunningi*	Coastal Mozambique.
Monticola	*rufocinereus*	*sclateri*	Arabian Peninsula; outside study area.
Monticola	*explorator*	*tenebriformes*	Lebombo Mountains; region excluded from analyses.
Saxicola	*torquatus*	*sibilla*	Madagascar; outside study area.
Saxicola	*torquatus*	*felix*	Arabian Peninsula; outside study area.
Saxicola	*torquatus*	*jebelmarrae*	Darfur; region excluded from analyses.
Saxicola	*torquatus*	*moptanus*	Senegal Delta to Inner Niger Delta.
Saxicola	*torquatus*	*voeltzkowi*	Grand Comoro Island; outside study area.
Thamnolaea	*cinnamomeiventris*	*kordofanensis*	Nuba Mountains; region excluded from analyses.
Oenanthe	*bottae*	*bottae*	Arabian Peninsula; outside study area.
Cinnyris	*habessinicus*	*hellmayri*	Arabian Peninsula; outside study area.
Cinnyris	*habessinicus*	*kinneari*	Arabian Peninsula; outside study area.

Continued on following page.

Table B.3, continued.

Genus	**Species**	**Subspecies**	**Excluded Reason**
Estrilda	*paludicola*	*ochrogaster*	Higher elevation population of a lowland taxa found in western Ethiopia and South Sudan. Excluded due to taxonomic affinities and uncertainty about complete distribution.
Anthus	*cinnamomeus*	*grotei*	Lower elevation mesic areas in Namibia and Botswana.
Anthus	*cinnamomeus*	*stabilis*	Sudanese highlands excluded from these analyses.
Anthus	*cinnamomeus*	*eximius*	Arabian Peninsula; outside study area.
Anthus	*similis*	*arabicus*	Arabian Peninsula; outside study area.
Anthus	*similis*	*captus*	Lebanon, Syria, Israel, Palestine and W Jordan; outside study area.
Anthus	*similis*	*decaptus*	Iran to India; outside study area.
Anthus	*similis*	*jerdoni*	Afghanistan to Bangladesh; outside study area.
Anthus	*similis*	*asbenaicus*	Mali and Niger.
Anthus	*similis*	*leucocraspedon*	Namibia to South Africa; region excluded from analyses.
Anthus	*similis*	*nicholsoni*	Botswana to South Africa; not montane.
Anthus	*similis*	*similis*	India; outside study area.
Anthus	*similis*	*travancoriensis*	India; outside study area.
Anthus	*similis*	*sokotrae*	Socotra; outside study area.

Continued on following page.

Table B.3, continued.

Genus	**Species**	**Subspecies**	**Excluded Reason**
Anthus	*similis*	*yamethini*	Myanmar; outside study area.

APPENDIX C

SUPPLEMENTAL FIGURES: GENETIC STRUCTURE, COMPARATIVE NICHE MODELING INFORM CONSERVATION PRIORITIES IN LACUSTRINE RIFT BIRDS

C.1 Introduction

Additional code for running these analyses and completing analyses and creating these figures can be found on Github at `https://github.com/jacobccooper/dissertation_appendices`. Code utilized the **R** packages *ggtree* [378], *phytools* [295], *raster* [157], *tidytree* [377], and *tidyverse* [370]. Images were contatenated for easier viewing using ImageMagick [337].

C.2 Supplementary Tables

Tables not shown here are available via `https://github.com/jacobccooper/dissertation_appendices`.

Table C.1: Sample list used for analyses of Lacustrine Rift birds. Species are listed here alphabetically to aid in finding samples. Please note that some coordinates here reflect location of massifs, and not necessarily exact locations used for niche modeling (see GBIF and eBird datasets).

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Batis diops*	385201	29.78	−1.23	Bwindi	
FMNH	*Batis diops*	385202	29.78	−1.23	Bwindi	
FMNH	*Batis diops*	385204	29.78	−1.23	Bwindi	
FMNH	*Batis diops*	385205	29.78	−1.23	Bwindi	
FMNH	*Batis diops*	450545	29.08	−4.99	Kabobo	
FMNH	*Batis diops*	450547	29.08	−4.99	Kabobo	
FMNH	*Batis diops*	WCS6	29.08	−4.99	Kabobo	
FMNH	*Batis diops*	441708	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	443926	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	443927	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	443928	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	443929	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	443930	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	481125	28.74	−2.32	Kahuzi-Biega	

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Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Batis diops*	KB34	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	KB50	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	KB53	28.74	−2.32	Kahuzi-Biega	
FMNH	*Batis diops*	346523	29.38	−2	Kibira-Nyungwe	
FMNH	*Batis diops*	346524	29.38	−2	Kibira-Nyungwe	
FMNH	*Batis diops*	346527	29.38	−2	Kibira-Nyungwe	
FMNH	*Batis diops*	358103	29.38	−2	Kibira-Nyungwe	
FMNH	*Batis diops*	358104	29.38	−2	Kibira-Nyungwe	
FMNH	*Batis diops*	358105	29.38	−2	Kibira-Nyungwe	
FMNH	*Batis diops*	358106	29.38	−2	Kibira-Nyungwe	
FMNH	*Batis diops*	355972	29.90	0.34	Rwenzori	Mahoma, 8 km NW Ibanda
FMNH	*Batis diops*	355973	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Batis diops*	355974	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda

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Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Batis diops*	355975	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Batis diops*	355976	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Batis diops*	355977	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Batis diops*	355978	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Batis diops*	437566	29.43	−0.14	W Rutanzige	
FMNH	*Batis molitor*					
FMNH	*Camaroptera brevicauda*	481147	28.90	−2.98	Itombwe	
FMNH	*Cinnyris regius*	385275	29.78	−1.23	Bwindi	
FMNH	*Cinnyris regius*	385276	29.78	−1.23	Bwindi	
FMNH	*Cinnyris regius*	385277	29.78	−1.23	Bwindi	
FMNH	*Cinnyris regius*	450580	29.08	−4.99	Kabobo	
FMNH	*Cinnyris regius*	450581	29.08	−4.99	Kabobo	

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Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cinnyris regius*	450582	29.08	−4.99	Kabobo	
FMNH	*Cinnyris regius*	450583	29.08	−4.99	Kabobo	
FMNH	*Cinnyris regius*	438857	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	441714	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	443948	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	443949	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	481228	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	481229	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	481230	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	481231	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	481232	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	481234	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	481235	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cinnyris regius*	346623	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris regius*	346624	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris regius*	346626	29.38	−2	Kibira-Nyungwe	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cinnyris regius*	346627	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris regius*	346631	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris regius*	346636	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris regius*	346649	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris regius*	358158	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris regius*	356179	29.90	0.34	Rwenzori	Choha, 6 km NW Ibanda
FMNH	*Cinnyris regius*	356181	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356184	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356205	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356206	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cinnyris regius*	356207	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356208	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356210	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356211	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356216	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356217	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356218	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356222	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cinnyris regius*	356226	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356256	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356257	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356267	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356268	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356270	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356271	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356272	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cinnyris regius*	356273	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356274	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356275	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356276	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356277	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356278	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356281	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356282	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cinnyris regius*	356289	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356290	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	356291	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Cinnyris regius*	KB40	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	385022	29.78	−1.23	Bwindi	
FMNH	*Cossypha archeri*	385023	29.78	−1.23	Bwindi	
FMNH	*Cossypha archeri*	385024	29.78	−1.23	Bwindi	
FMNH	*Cossypha archeri*	385025	29.78	−1.23	Bwindi	
FMNH	*Cossypha archeri*	438819	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	438820	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	443844	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	443845	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	443846	28.74	−2.32	Kahuzi-Biega	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cossypha archeri*	443847	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	443848	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	443849	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	481187	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	481188	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	481189	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	481190	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	481191	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	358029	29.38	−2	Kibira-Nyungwe	
FMNH	*Cossypha archeri*	355601	29.90	0.34	Rwenzori	
FMNH	*Cossypha archeri*	355602	29.90	0.34	Rwenzori	
FMNH	*Cossypha archeri*	355603	29.90	0.34	Rwenzori	
FMNH	*Cossypha archeri*	355604	29.90	0.34	Rwenzori	
FMNH	*Cossypha archeri*	355606	29.90	0.34	Rwenzori	
FMNH	*Cossypha archeri*	355608	29.90	0.34	Rwenzori	
FMNH	*Cossypha archeri*	355609	29.90	0.34	Rwenzori	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cossypha archeri*	355613	29.90	0.34	Rwenzori	
FMNH	*Cossypha archeri*	KB11	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cossypha archeri*	WCS8	29.08	−4.99	Kabobo	
FMNH	*Cossypha archeri*	450492	29.08	−4.99	Kabobo	ND2 only
FMNH	*Cossyphicula roberti*	450491	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	385258	29.78	−1.23	Bwindi	
FMNH	*Cyanomitra alinae*	385259	29.78	−1.23	Bwindi	
FMNH	*Cyanomitra alinae*	385260	29.78	−1.23	Bwindi	
FMNH	*Cyanomitra alinae*	385261	29.78	−1.23	Bwindi	
FMNH	*Cyanomitra alinae*	385262	29.78	−1.23	Bwindi	
FMNH	*Cyanomitra alinae*	481250	28.90	−2.98	Itombwe	
FMNH	*Cyanomitra alinae*	481256	28.90	−2.98	Itombwe	
FMNH	*Cyanomitra alinae*	450557	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450558	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450559	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450560	29.08	−4.99	Kabobo	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cyanomitra alinae*	450561	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450562	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450563	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450564	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450565	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	450566	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	438852	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	438853	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	438854	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	438855	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	438877	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	438878	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	438879	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	441710	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	441711	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	443941	28.74	−2.32	Kahuzi-Biega	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cyanomitra alinae*	443942	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	443943	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	443944	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	443945	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	443946	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	481248	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	481249	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	481251	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	481252	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	481253	28.74	−2.32	Kahuzi-Biega	
FMNH	*Cyanomitra alinae*	346590	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	346591	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	346592	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	346594	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	358146	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	358148	29.38	−2	Kibira-Nyungwe	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cyanomitra alinae*	355996	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	355997	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	355998	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	355999	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356008	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356020	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356022	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356027	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356037	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356039	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356056	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356059	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356060	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356061	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356064	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356081	29.90	0.34	Rwenzori	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Cyanomitra alinae*	356082	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356083	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356084	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	356085	29.90	0.34	Rwenzori	
FMNH	*Cyanomitra alinae*	JCK6614	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	JCK6630	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	JCK6717	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	JCK6757	29.38	−2	Kibira-Nyungwe	
FMNH	*Cyanomitra alinae*	WCS3	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	WCS3	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra alinae*	WCS4	29.08	−4.99	Kabobo	
FMNH	*Cyanomitra verticalis*	440904	33.81	−10.58	Nyika	
FMNH	*Graueria vittata*	441704	28.74	−2.32	Kahuzi-Biega	
FMNH	*Graueria vittata*	443913	28.74	−2.32	Kahuzi-Biega	
FMNH	*Graueria vittata*	443914	28.74	−2.32	Kahuzi-Biega	
FMNH	*Graueria vittata*	385149	29.38	−2	Kibira-Nyungwe	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Graueria vittata*	385150	29.38	−2	Kibira-Nyungwe	
FMNH	*Serinus frontalis*	DRC239				
AMNH	*Iduna similis*	827030	29.78	−1.23	Bwindi	
FMNH	*Iduna similis*	262897	29.42	−1.46	Bwindi	Central Kivu volcanoes
FMNH	*Iduna similis*	262901	29.42	−1.46	Bwindi	Wrong series
FMNH	*Iduna similis*	385103	29.78	−1.23	Bwindi	
FMNH	*Iduna similis*	385104	29.78	−1.23	Bwindi	
FMNH	*Iduna similis*	385105	29.78	−1.23	Bwindi	
FMNH	*Iduna similis*	391776	31.54	1.67	E.Albert	
FMNH	*Iduna similis*	298666	32.93	3.97	Imatong	Gilo area
FMNH	*Iduna similis*	298667	32.93	3.97	Imatong	Gilo area
FMNH	*Iduna similis*	298668	32.93	3.97	Imatong	Gilo area
FMNH	*Iduna similis*	298669	32.93	3.97	Imatong	Gilo area
FMNH	*Iduna similis*	298672	32.93	3.97	Imatong	Gilo area

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Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
AMNH	*Iduna similis*	608882	29.04	−3.63	Itombwe	W of Tanganyika (Grauer)
AMNH	*Iduna similis*	608888	29.04	−3.63	Itombwe	W of Baraka (Grauer)
FMNH	*Iduna similis*	481167	28.90	−2.98	Itombwe	
FMNH	*Iduna similis*	481169	28.90	−2.98	Itombwe	
FMNH	*Iduna similis*	481170	28.90	−2.98	Itombwe	
FMNH	*Iduna similis*	443885	28.74	−2.32	Kahuzi-Biega	
FMNH	*Iduna similis*	481168	28.74	−2.32	Kahuzi-Biega	
FMNH	*Iduna similis*	346426	29.38	−2	Kibira-Nyungwe	
FMNH	*Iduna similis*	350866	29.38	−2	Kibira-Nyungwe	
FMNH	*Iduna similis*	440695	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	440696	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	440697	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	440698	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	440699	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	440700	33.81	−10.58	Nyika	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Iduna similis*	440701	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	440702	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	440703	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468238	33.44	−11.04	Nyika	Vwaza Wildlife Reserve
FMNH	*Iduna similis*	468239	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468240	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468241	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468242	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468243	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468244	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468245	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468246	33.44	−11.04	Nyika	Vwaza Wildlife Reserve
FMNH	*Iduna similis*	468247	33.81	−10.58	Nyika	
FMNH	*Iduna similis*	468248	33.81	−10.58	Nyika	Runyina Bridge

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Iduna similis*	262893	29.90	0.34	Rwenzori	
FMNH	*Iduna similis*	262894	29.90	0.34	Rwenzori	
FMNH	*Iduna similis*	262895	29.90	0.34	Rwenzori	
FMNH	*Iduna similis*	262896	29.90	0.34	Rwenzori	
FMNH	*Iduna similis*	355779	29.90	0.34	Rwenzori	Mahoma, 8 km NW Ibanda
FMNH	*Iduna similis*	355780	29.90	0.34	Rwenzori	Mahoma, 8 km NW Ibanda
FMNH	*Iduna similis*	355786	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Iduna similis*	355787	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Iduna similis*	355788	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Iduna similis*	355789	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Iduna similis*	355790	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Iduna similis*	355792	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Iduna similis*	355798	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Iduna similis*	355799	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Oreolais ruwenzorii*	385140	29.78	−1.23	Bwindi	
FMNH	*Oreolais ruwenzorii*	438834	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	441701	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	441702	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	443905	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	443906	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	443907	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	443908	28.74	−2.32	Kahuzi-Biega	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Oreolais ruwenzorii*	481120	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	481121	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	481123	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	481124	28.74	−2.32	Kahuzi-Biega	
FMNH	*Oreolais ruwenzorii*	346468	29.38	−2	Kibira-Nyungwe	
FMNH	*Oreolais ruwenzorii*	346474	29.38	−2	Kibira-Nyungwe	
FMNH	*Oreolais ruwenzorii*	358084	29.38	−2	Kibira-Nyungwe	
FMNH	*Oreolais ruwenzorii*	355835	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355837	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355848	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355849	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355856	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355858	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355864	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355868	29.90	0.34	Rwenzori	
FMNH	*Oreolais ruwenzorii*	355869	29.90	0.34	Rwenzori	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Phylloscopus laetus*	385174	29.78	−1.23	Bwindi	
FMNH	*Phylloscopus laetus*	385175	29.78	−1.23	Bwindi	
FMNH	*Phylloscopus laetus*	385176	29.78	−1.23	Bwindi	
AMNH	*Phylloscopus laetus*	178193	29.04	−3.63	Itombwe	
AMNH	*Phylloscopus laetus*	262885	29.04	−3.63	Itombwe	
FMNH	*Phylloscopus laetus*	450530	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450531	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450598	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450601	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450602	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450603	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450604	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450605	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450606	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450607	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450608	29.08	−4.99	Kabobo	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Phylloscopus laetus*	450610	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450611	29.08	−4.99	Kabobo	
FMNH	*Phylloscopus laetus*	450612	29.08	−4.99	Kabobo	
AMNH	*Phylloscopus laetus*	764646	28.74	−2.32	Kahuzi-Biega	
FMNH	*Phylloscopus laetus*	438837	28.74	−2.32	Kahuzi-Biega	
FMNH	*Phylloscopus laetus*	443920	28.74	−2.32	Kahuzi-Biega	
FMNH	*Phylloscopus laetus*	443921	28.74	−2.32	Kahuzi-Biega	
FMNH	*Phylloscopus laetus*	443922	28.74	−2.32	Kahuzi-Biega	
FMNH	*Phylloscopus laetus*	443923	28.74	−2.32	Kahuzi-Biega	
FMNH	*Phylloscopus laetus*	443924	28.74	−2.32	Kahuzi-Biega	
FMNH	*Phylloscopus laetus*	346427	29.38	−2	Kibira-Nyungwe	
FMNH	*Phylloscopus laetus*	346428	29.38	−2	Kibira-Nyungwe	
FMNH	*Phylloscopus laetus*	346429	29.38	−2	Kibira-Nyungwe	
FMNH	*Phylloscopus laetus*	358061	29.38	−2	Kibira-Nyungwe	
FMNH	*Phylloscopus laetus*	358062	29.38	−2	Kibira-Nyungwe	
FMNH	*Phylloscopus laetus*	358063	29.38	−2	Kibira-Nyungwe	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
AMNH	*Phylloscopus laetus*	262875	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262876	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262877	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262879	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262880	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262881	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262883	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262884	29.90	0.34	Rwenzori	
FMNH	*Phylloscopus laetus*	355933	29.90	0.34	Rwenzori	
FMNH	*Phylloscopus laetus*	355934	29.90	0.34	Rwenzori	
FMNH	*Phylloscopus laetus*	355938	29.90	0.34	Rwenzori	
FMNH	*Phylloscopus laetus*	355940	29.90	0.34	Rwenzori	
FMNH	*Phylloscopus laetus*	355942	29.90	0.34	Rwenzori	
FMNH	*Phylloscopus laetus*	355943	29.90	0.34	Rwenzori	
AMNH	*Phylloscopus laetus*	262878	29.43	−0.14	W Rutanzige	
FMNH	*Phylloscopus laetus*	KB41	28.74	−2.32	Kahuzi-Biega	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Phylloscopus umbrovirens*	355951	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	385383	29.78	−1.23	Bwindi	
FMNH	*Ploceus alienus*	438866	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	438867	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	438868	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	441723	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	441724	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443968	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443969	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443970	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443971	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443972	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443973	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443974	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443975	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	443976	28.74	−2.32	Kahuzi-Biega	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Ploceus alienus*	481274	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	481275	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	481276	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	481277	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	481278	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus alienus*	346742	29.38	−2	Kibira-Nyungwe	
FMNH	*Ploceus alienus*	358207	29.38	−2	Kibira-Nyungwe	
FMNH	*Ploceus alienus*	358208	29.38	−2	Kibira-Nyungwe	
FMNH	*Ploceus alienus*	358209	29.38	−2	Kibira-Nyungwe	
FMNH	*Ploceus alienus*	356517	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356518	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356519	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356521	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356522	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356524	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356530	29.90	0.34	Rwenzori	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Ploceus alienus*	356533	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356534	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356535	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356537	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356541	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356547	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356548	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	356549	29.90	0.34	Rwenzori	
FMNH	*Ploceus alienus*	KB12	28.74	−2.32	Kahuzi-Biega	
FMNH	*Ploceus olivaceiceps*	444508	34.00	−13.38	Ntchisi	
FMNH	*Sylvia abyssinica*	468139	33.81	−10.58	Nyika	
FMNH	*Sylvia abyssinica*	468140	33.81	−10.58	Nyika	
FMNH	*Sylvia abyssinica*	468141	33.81	−10.58	Nyika	
FMNH	*Sylvia abyssinica*	468142	33.81	−10.58	Nyika	
FMNH	*Sylvia abyssinica*	468143	33.81	−10.58	Nyika	
AMNH	*Sylvia atriceps*	588868	29.42	−1.46	Bwindi	Mt Mikeno

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
AMNH	*Sylvia atriceps*	588869	29.42	−1.46	Bwindi	Mt Mikeno
AMNH	*Sylvia atriceps*	588870	29.42	−1.46	Bwindi	Vulkane Kivu
AMNH	*Sylvia atriceps*	588871	29.42	−1.46	Bwindi	Vulkane Kivu
AMNH	*Sylvia atriceps*	588872	29.42	−1.46	Bwindi	Vulkane Kivu
FMNH	*Sylvia atriceps*	196187	29.78	−1.23	Bwindi	Kagezi, Rwanda
FMNH	*Sylvia atriceps*	385071	29.78	−1.23	Bwindi	
FMNH	*Sylvia atriceps*	385072	29.78	−1.23	Bwindi	
FMNH	*Sylvia atriceps*	385073	29.78	−1.23	Bwindi	
FMNH	*Sylvia atriceps*	385074	29.78	−1.23	Bwindi	
AMNH	*Sylvia atriceps*	196627	29.04	−3.63	Itombwe	W Lake Tang
AMNH	*Sylvia atriceps*	409970	28.90	−2.98	Itombwe	
AMNH	*Sylvia atriceps*	409971	28.90	−2.98	Itombwe	three days south
AMNH	*Sylvia atriceps*	588878	28.90	−2.98	Itombwe	
AMNH	*Sylvia atriceps*	588879	29.04	−3.63	Itombwe	W Lake Tang
AMNH	*Sylvia atriceps*	588880	29.04	−3.63	Itombwe	W Lake Tang
AMNH	*Sylvia atriceps*	588881	28.90	−2.98	Itombwe	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
AMNH	*Sylvia atriceps*	588883	29.04	−3.63	Itombwe	Near Baraka
AMNH	*Sylvia atriceps*	588885	29.04	−3.63	Itombwe	Near Baraka
FMNH	*Sylvia atriceps*	95528	29.04	−3.63	Itombwe	W Lake Tang
FMNH	*Sylvia atriceps*	484114	29.04	−3.63	Itombwe	S Lusaka
FMNH	*Sylvia atriceps*	484115	29.04	−3.63	Itombwe	S Lusaka
AMNH	*Sylvia atriceps*	200215	28.74	−2.32	Kahuzi-Biega	
AMNH	*Sylvia atriceps*	764430	28.74	−2.32	Kahuzi-Biega	
AMNH	*Sylvia atriceps*	764431	28.74	−2.32	Kahuzi-Biega	
AMNH	*Sylvia atriceps*	764432	28.74	−2.32	Kahuzi-Biega	
AMNH	*Sylvia atriceps*	764433	28.74	−2.32	Kahuzi-Biega	
AMNH	*Sylvia atriceps*	764434	28.74	−2.32	Kahuzi-Biega	
AMNH	*Sylvia atriceps*	764436	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	437572	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	437573	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	438824	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	441696	28.74	−2.32	Kahuzi-Biega	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Sylvia atriceps*	441697	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	443878	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	443879	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	443880	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	443881	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481202	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481203	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481204	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481205	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481206	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481208	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481209	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvia atriceps*	481210	28.74	−2.32	Kahuzi-Biega	
AMNH	*Sylvia atriceps*	588864	29.38	−2	Kibira-Nyungwe	Nyungwe
AMNH	*Sylvia atriceps*	588866	29.38	−2	Kibira-Nyungwe	Nyungwe
AMNH	*Sylvia atriceps*	588867	29.38	−2	Kibira-Nyungwe	Nyungwe

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Sylvia atriceps*	346422	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvia atriceps*	350881	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvia atriceps*	358055	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvia atriceps*	358056	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvia atriceps*	358059	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvia atriceps*	358060	29.38	−2	Kibira-Nyungwe	
AMNH	*Sylvia atriceps*	263173	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	263174	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	263175	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	263176	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	263178	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	263179	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	588874	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	588875	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	588876	29.90	0.34	Rwenzori	
AMNH	*Sylvia atriceps*	588877	29.90	0.34	Rwenzori	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Sylvia atriceps*	196189	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	196190	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	196192	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355697	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355702	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355705	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355713	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355723	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355724	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355726	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355731	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	355734	29.90	0.34	Rwenzori	
FMNH	*Sylvia atriceps*	KB15	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	385153	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	385154	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	385155	29.78	−1.23	Bwindi	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Sylvietta leucophrys*	385156	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	385157	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	385158	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	385159	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	385160	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	395976	29.78	−1.23	Bwindi	
FMNH	*Sylvietta leucophrys*	481159	28.90	−2.98	Itombwe	
FMNH	*Sylvietta leucophrys*	481161	28.90	−2.98	Itombwe	
FMNH	*Sylvietta leucophrys*	481162	28.90	−2.98	Itombwe	
FMNH	*Sylvietta leucophrys*	450529	29.08	−4.99	Kabobo	
FMNH	*Sylvietta leucophrys*	438830	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	438831	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	443915	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	443916	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	443917	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	443918	28.74	−2.32	Kahuzi-Biega	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Sylvietta leucophrys*	443919	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	481157	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	481158	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	481160	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	346500	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvietta leucophrys*	346508	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvietta leucophrys*	358090	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvietta leucophrys*	358092	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvietta leucophrys*	355890	29.90	0.34	Rwenzori	Choha, 6 km NW Ibanda
FMNH	*Sylvietta leucophrys*	355892	29.90	0.34	Rwenzori	Choha, 6 km NW Ibanda
FMNH	*Sylvietta leucophrys*	355894	29.90	0.34	Rwenzori	
FMNH	*Sylvietta leucophrys*	355895	29.90	0.34	Rwenzori	Choha, 6 km NW Ibanda
FMNH	*Sylvietta leucophrys*	355896	29.90	0.34	Rwenzori	

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Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Sylvietta leucophrys*	355898	29.90	0.34	Rwenzori	
FMNH	*Sylvietta leucophrys*	355899	29.90	0.34	Rwenzori	
FMNH	*Sylvietta leucophrys*	355902	29.90	0.34	Rwenzori	
FMNH	*Sylvietta leucophrys*	355903	29.90	0.34	Rwenzori	Choha, 6 km NW Ibanda
FMNH	*Sylvietta leucophrys*	355924	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Sylvietta leucophrys*	355928	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Sylvietta leucophrys*	355929	29.90	0.34	Rwenzori	Nyabitaba, 10 km NW Ibanda
FMNH	*Sylvietta leucophrys*	JCK6627	29.38	−2	Kibira-Nyungwe	
FMNH	*Sylvietta leucophrys*	KB18	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta leucophrys*	KB49	28.74	−2.32	Kahuzi-Biega	
FMNH	*Sylvietta whytii*	474887	35.46	−14.42	Mangochi Hills	
	Chamaetylas choloensis					

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Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
	Chamaetylas fulleborni					
FMNH	*Chamaetylas poliophrys*	450512	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450511	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450510	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450509	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450507	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450506	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450505	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450504	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450503	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450502	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450501	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450500	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450499	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450498	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	450497	29.08	−4.99	Kabobo	

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Table C.1, continued.

Collection	Species	Sample	Longitude	Latitude	Meta-locality	Note
FMNH	*Chamaetylas poliophrys*	450496	29.08	−4.99	Kabobo	
FMNH	*Chamaetylas poliophrys*	443856	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	443854	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	443853	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	443852	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	443851	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	443850	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	441688	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	438818	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	438817	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	438816	28.74	−2.32	Kahuzi-Biega	
FMNH	*Chamaetylas poliophrys*	437548	29.43	−0.14	W Rutanzige	
FMNH	*Chamaetylas poliophrys*	385038	29.78	−1.23	Bwindi	
FMNH	*Chamaetylas poliophrys*	385037	29.78	−1.23	Bwindi	
FMNH	*Chamaetylas poliophrys*	385036	29.78	−1.23	Bwindi	
FMNH	*Chamaetylas poliophrys*	385035	29.78	−1.23	Bwindi	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Chamaetylas poliophrys*	385034	29.78	−1.23	Bwindi	
FMNH	*Chamaetylas poliophrys*	385032	29.78	−1.23	Bwindi	
FMNH	*Chamaetylas poliophrys*	385031	29.78	−1.23	Bwindi	
FMNH	*Chamaetylas poliophrys*	385029	29.78	−1.23	Bwindi	
FMNH	*Chamaetylas poliophrys*	358038	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	358037	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	358035	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	358034	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	358032	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	358031	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	358030	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	355643	29.90	0.34	Rwenzori	
FMNH	*Chamaetylas poliophrys*	355634	29.90	0.34	Rwenzori	
FMNH	*Chamaetylas poliophrys*	355633	29.90	0.34	Rwenzori	
FMNH	*Chamaetylas poliophrys*	355628	29.90	0.34	Rwenzori	
FMNH	*Chamaetylas poliophrys*	355627	29.90	0.34	Rwenzori	

Continued on following page.

Table C.1, continued.

Collection	**Species**	**Sample**	**Longitude**	**Latitude**	**Meta-locality**	**Note**
FMNH	*Chamaetylas poliophrys*	355623	29.90	0.34	Rwenzori	
FMNH	*Chamaetylas poliophrys*	355621	29.90	0.34	Rwenzori	
FMNH	*Chamaetylas poliophrys*	355619	29.90	0.34	Rwenzori	
FMNH	*Chamaetylas poliophrys*	346401	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	346400	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	346395	29.38	−2	Kibira-Nyungwe	
FMNH	*Chamaetylas poliophrys*	346394	29.38	−2	Kibira-Nyungwe	
FMNH	*Cinnyris reichenowi*	385278	29.78	−1.23	Bwindi	
KU	*Cinnyris preussi*	131883				

C.3 Genetic analyses

The following are figures corresponding to the genetic analyses.

C.3.1 Haplotype median joining networks

The following are haplotype networks generated for species in the Lacustrine Rift.

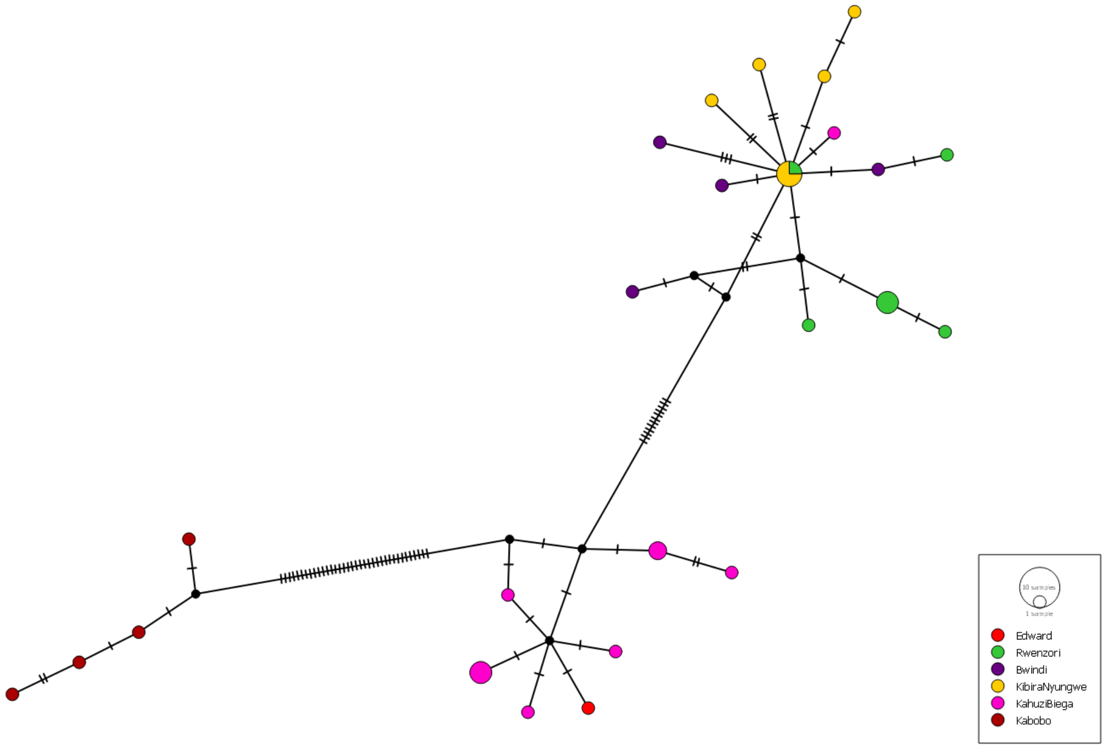

Figure C.1: *Batis diops* haplotype network based on ND2 genes. Note that despite the genetic differentiation observed in Mt. Kabobo populations of Batis diops, there are no described subspecies within this complex. There is also one individual from Kahuzi-Biega (West Rift) that is a member of the East Rift haplotype group.

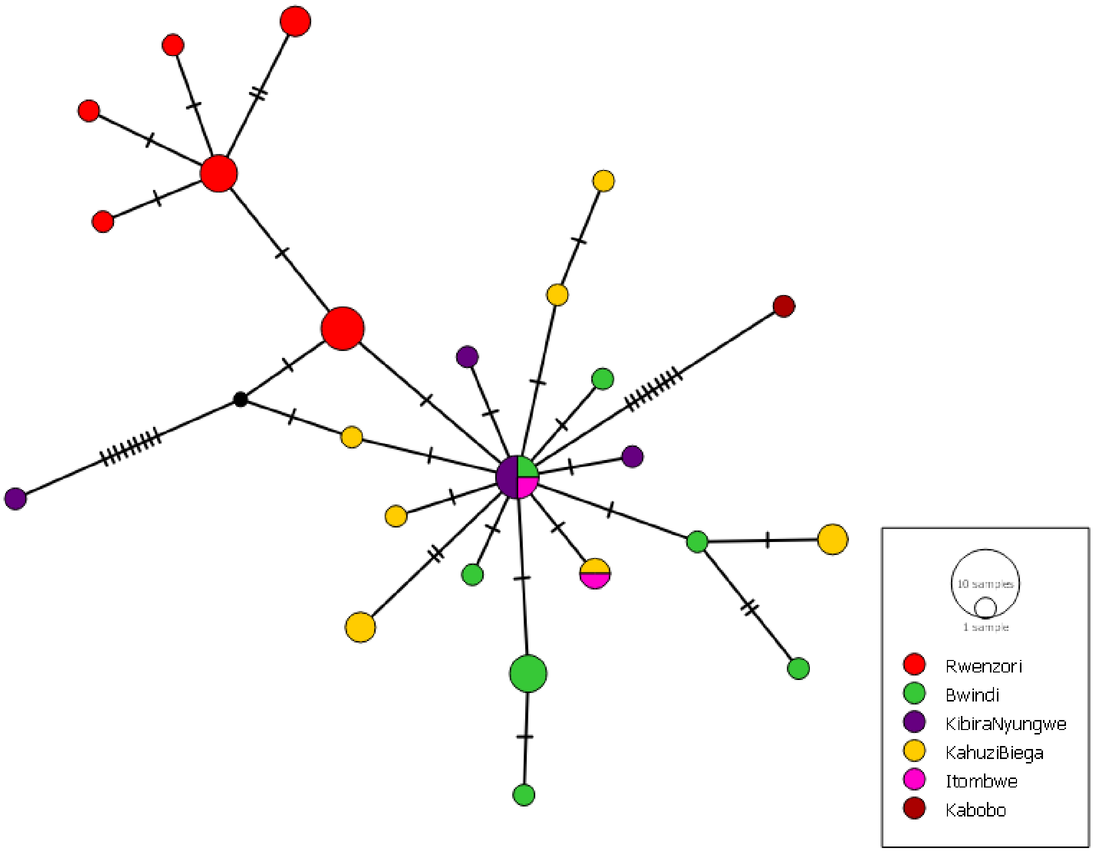

Figure C.2: *Sylvietta leucophrys* haplotype net work based on ND2 genes. Birds from the Rwenzori Mountains are part of the nominate subspecies (along with East Africa populations not included here), whereas the rest of the Lacustrine Rift (with the exception of the Lendu Plateau) is occupied by the subspecies *chloronota*. The Lendu Plateau population, *S. l. chapini*, was not included in this study and is sometimes split as a separate species.

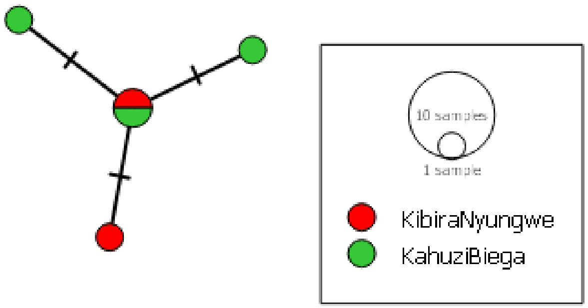

Figure C.3: *Graueria vittata* haplotype network based on ND2 genes.

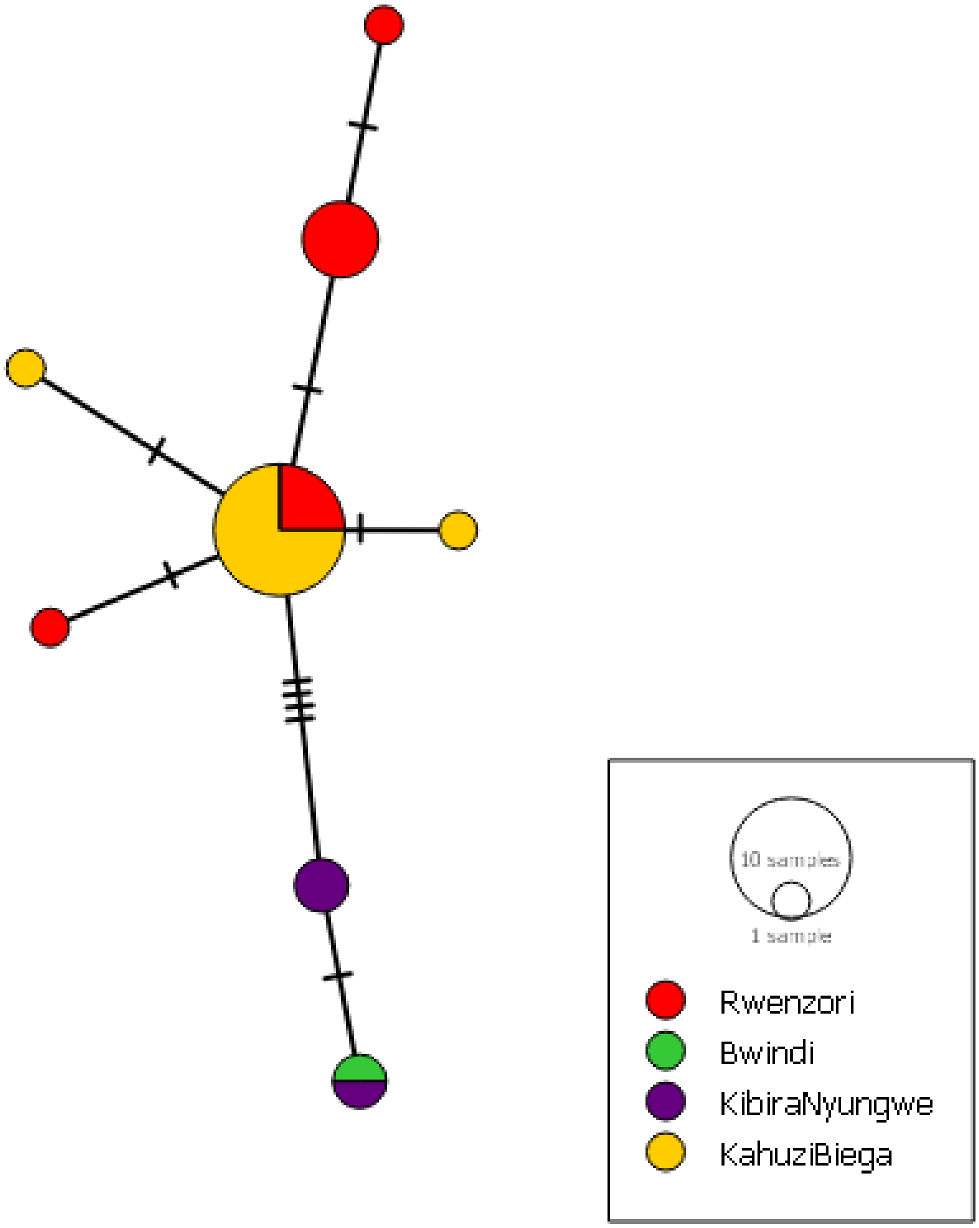

Figure C.4: *Oreolais ruwenzorii* haplotype network based on ND2 genes.

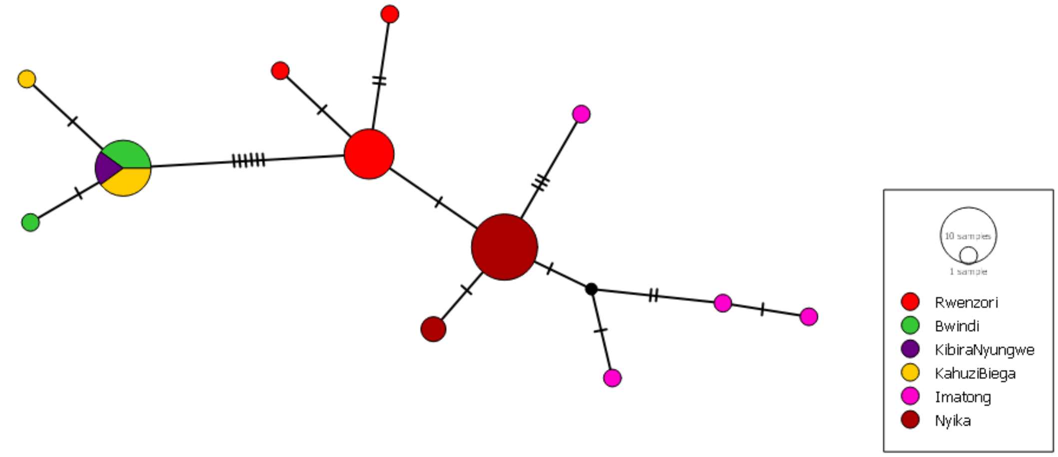

Figure C.5: *Iduna similis* haplotype network based on ND2 genes. Note the apparent similarity of the Rwenzori Mountains to the Nyika Highlands of Malawi and the Imatong Mountains of South Sudan & Uganda.

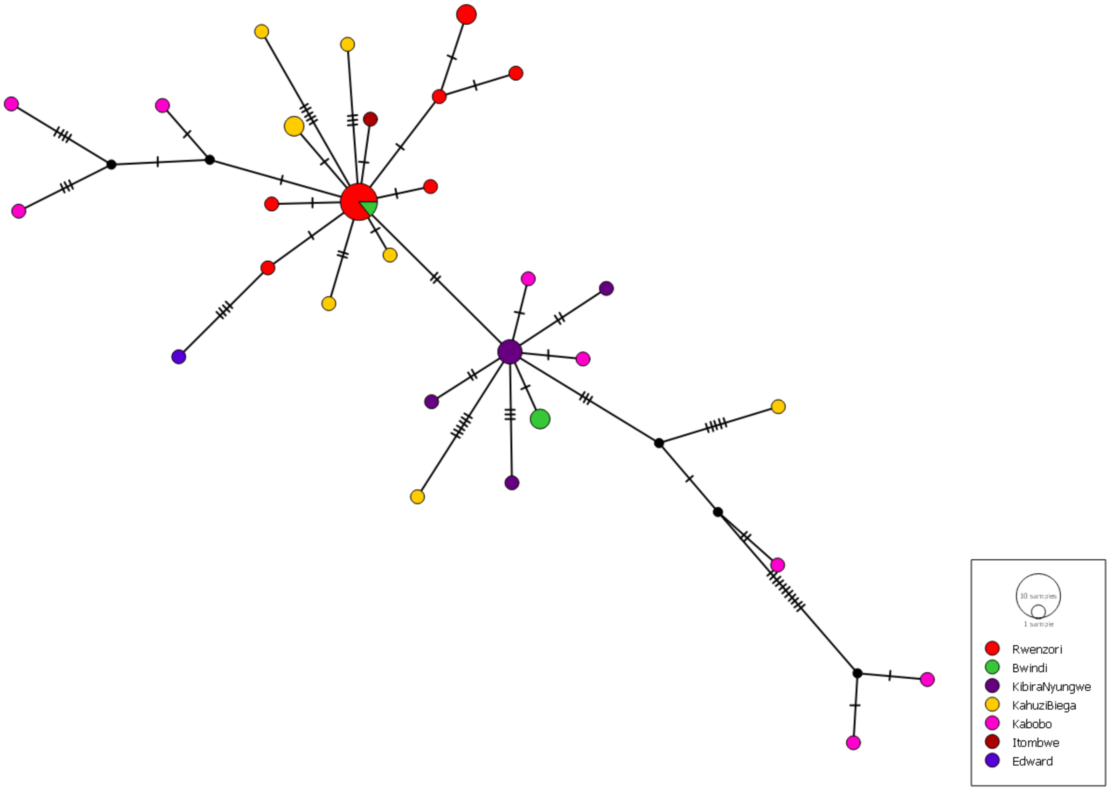

Figure C.6: *Phylloscopus laetus* haplotype network using ND2 genes. Note the fairly panmictic nature of the tree, especially with respect to Mt. Kabobo individuals being recovered in clusters with most other haplotype groups, despite the geographic isolation of Mt. Kabobo. It is worth noting that individuals from Mt. Kabobo are described as a separate subspecies (*schoutedeni*).

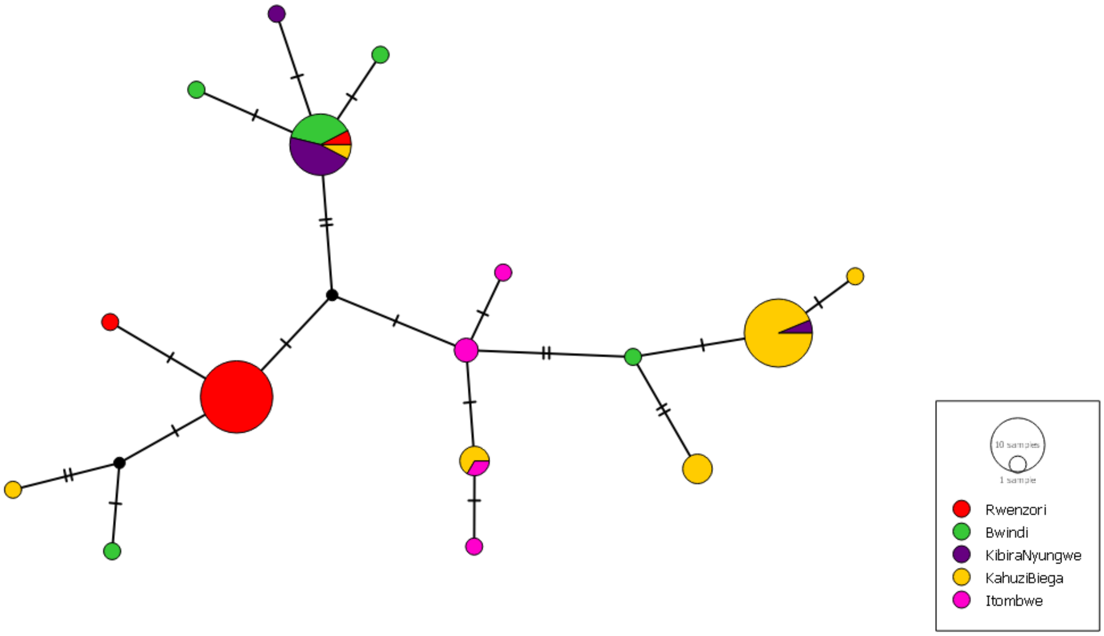

Figure C.7: *Sylvia atriceps* haplotype network using ND2 genes.

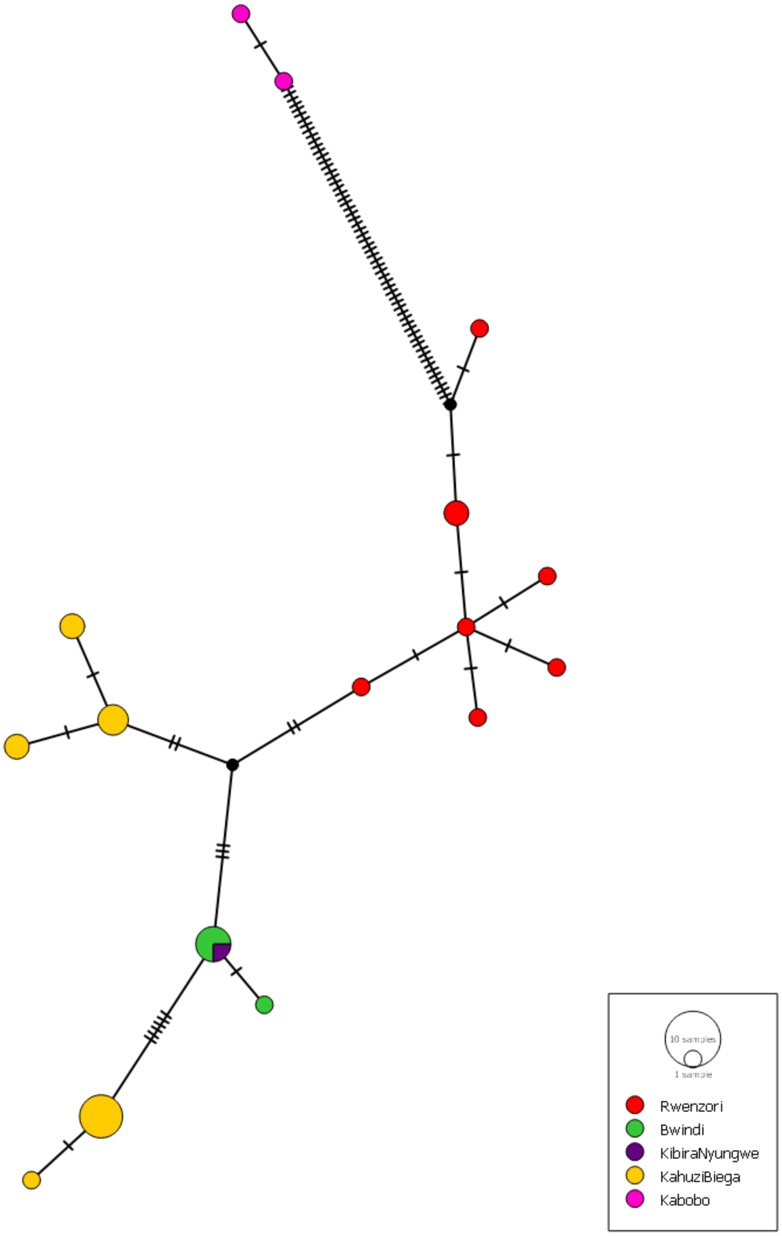

Figure C.8: *Cossypha archeri* haplotype network using ND2 genes. Note the distinctiveness of birds from Mt. Kabobo, a presently recognized subspecies that we elevate to species level (*C. kimbutui*).

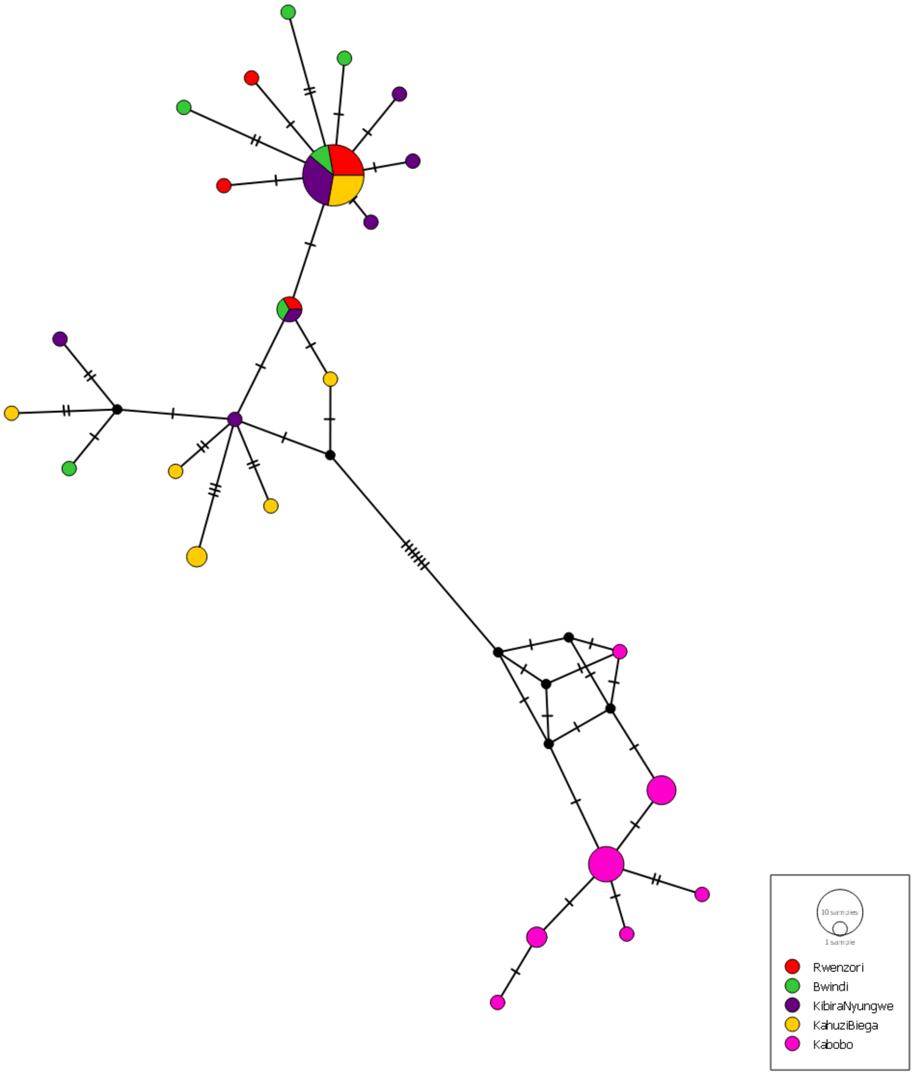

Figure C.9: *Chamaetylas poliophrys* haplotype network using ND2 genes. Note that we elevate the Mt. Kabobo subspecies to species rank, *Chamaetylas kaboboensis*.

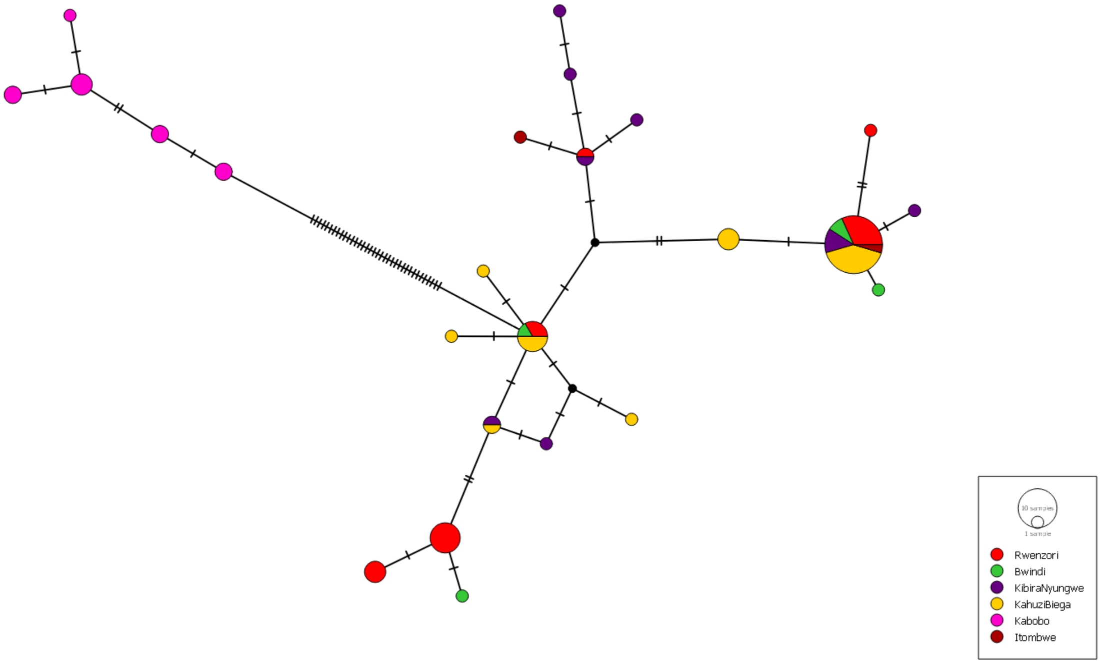

Figure C.10: *Cyanomitra alinae* haplotype network based on ND2 genes. Note the apparently panmictic nature of main Lacustrine Rift populations, despite two described subspecies being represented within this group (*C. a. alinae* of the Rwenzori mountains and the Eastern Rift and *C. a. tanganjicae* of the Western Rift). We elevate southern populations to species rank as *C. k. kaboboensis*, tentatively including *C. k. marungensis* as a subspecies.

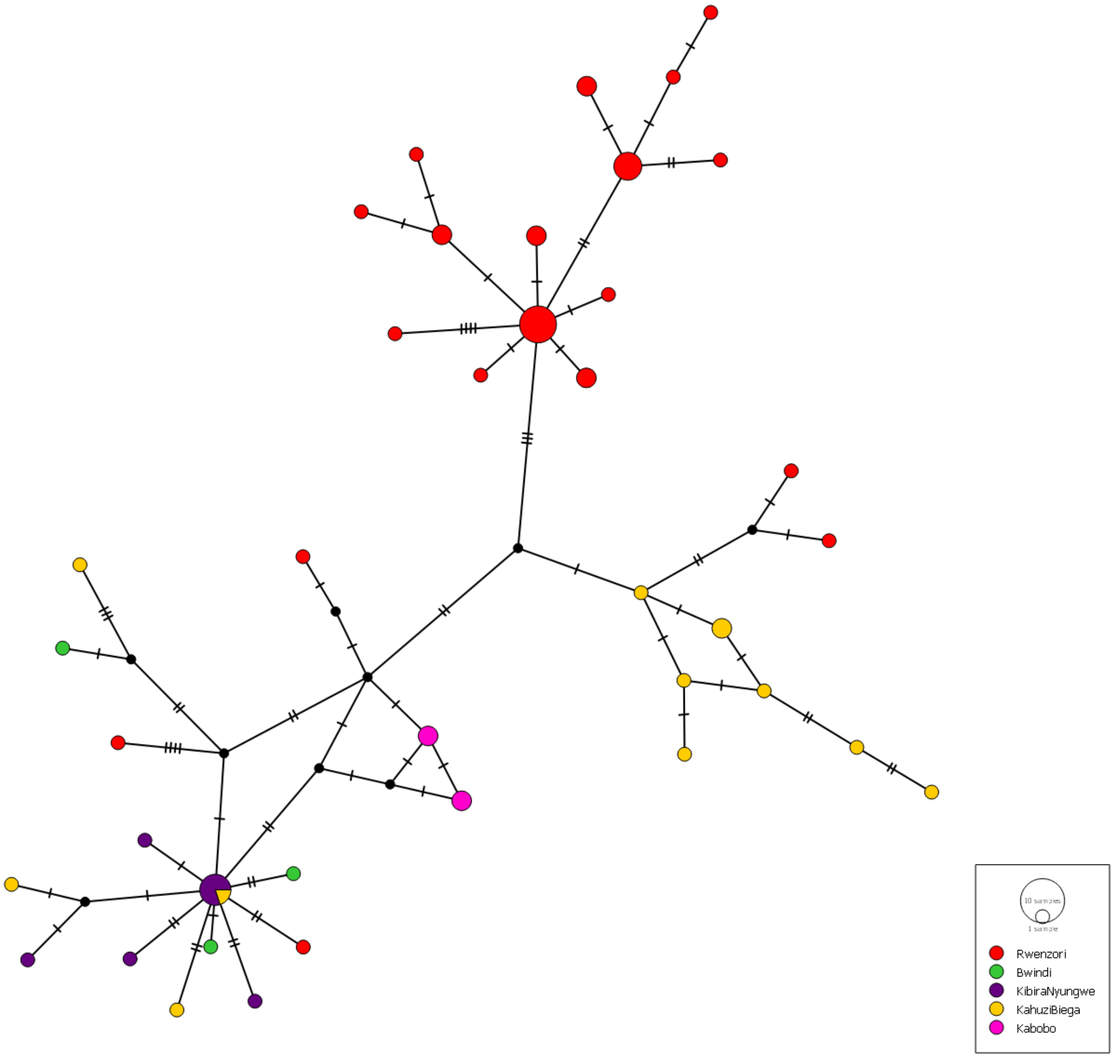

Figure C.11: *Cinnyris regius* haplotype network using ND2 genes. All samples are from the subspecies *C. r. regius*.

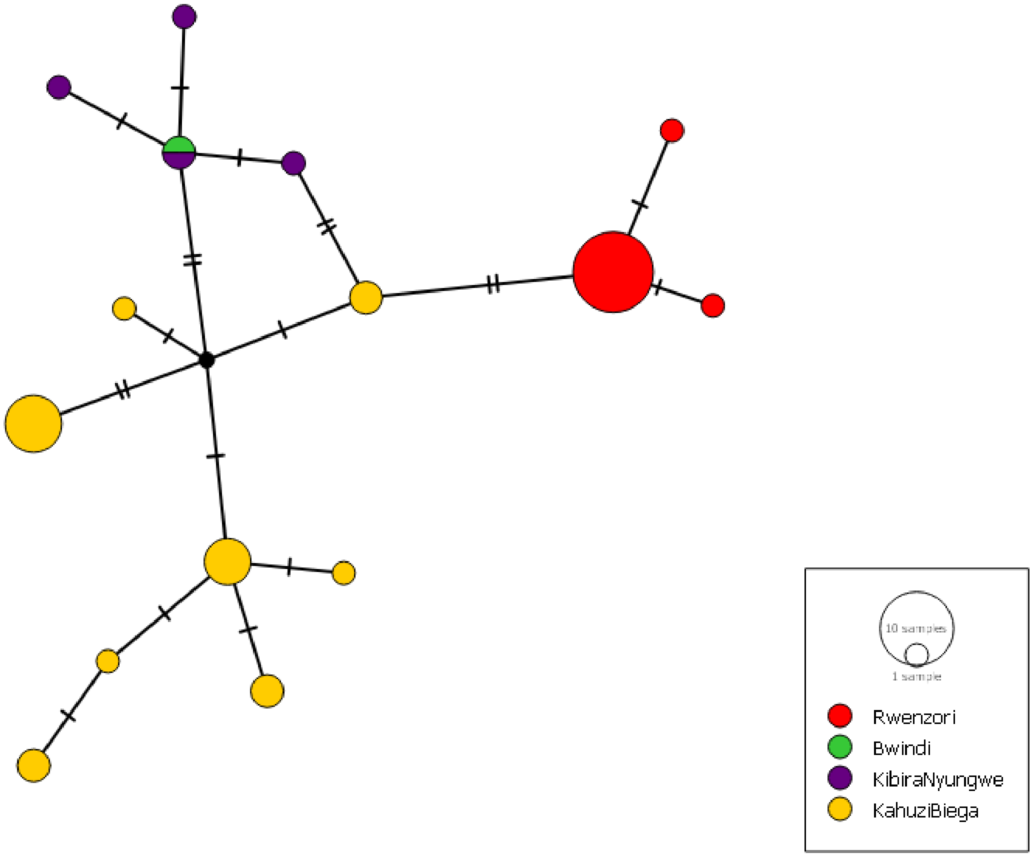

Figure C.12: *Ploceus alienus* haplotype network created using ND2 genes.

C.3.2 BEAST trees

Time-calibrated BEAST trees for Lacustrine Rift taxa.

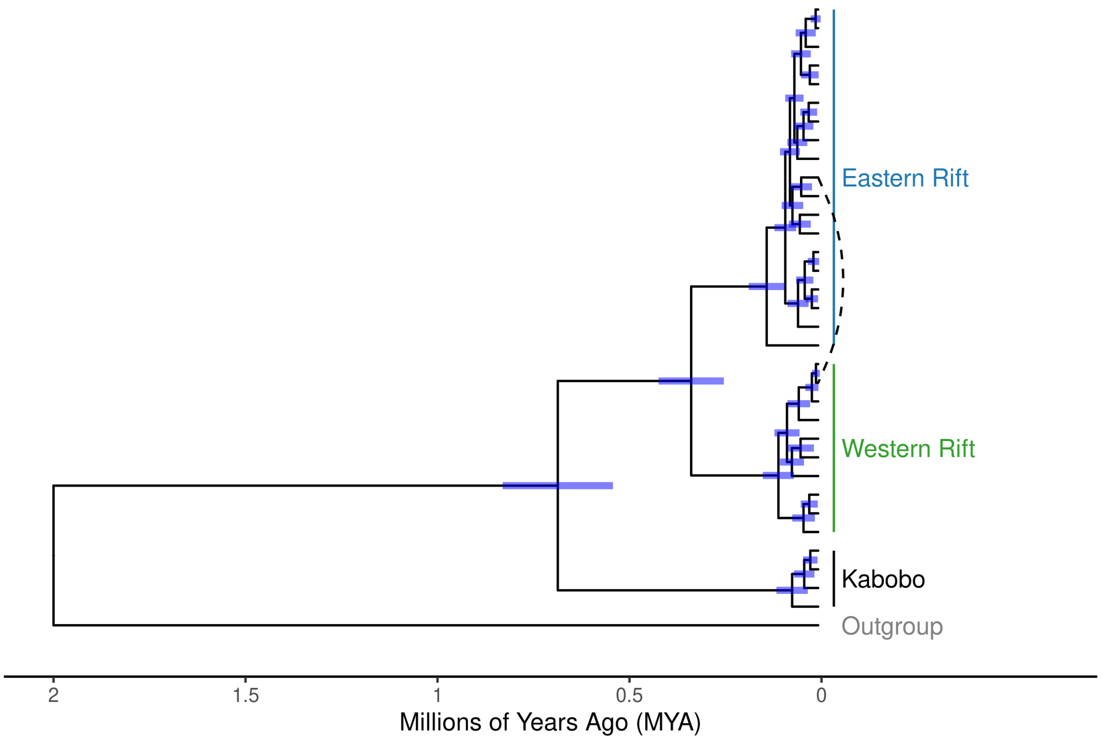

Figure C.13: *Batis diops* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Batis molitor*. Note that birds from Mt. Kabobo are not presently described as a separate subspecies from the rest of the Lacustrine Rift. The dashed line connects the Western Rift individual with an Eastern haplotype to an arbitrary eastern individual to illustrate the observed connectivity.

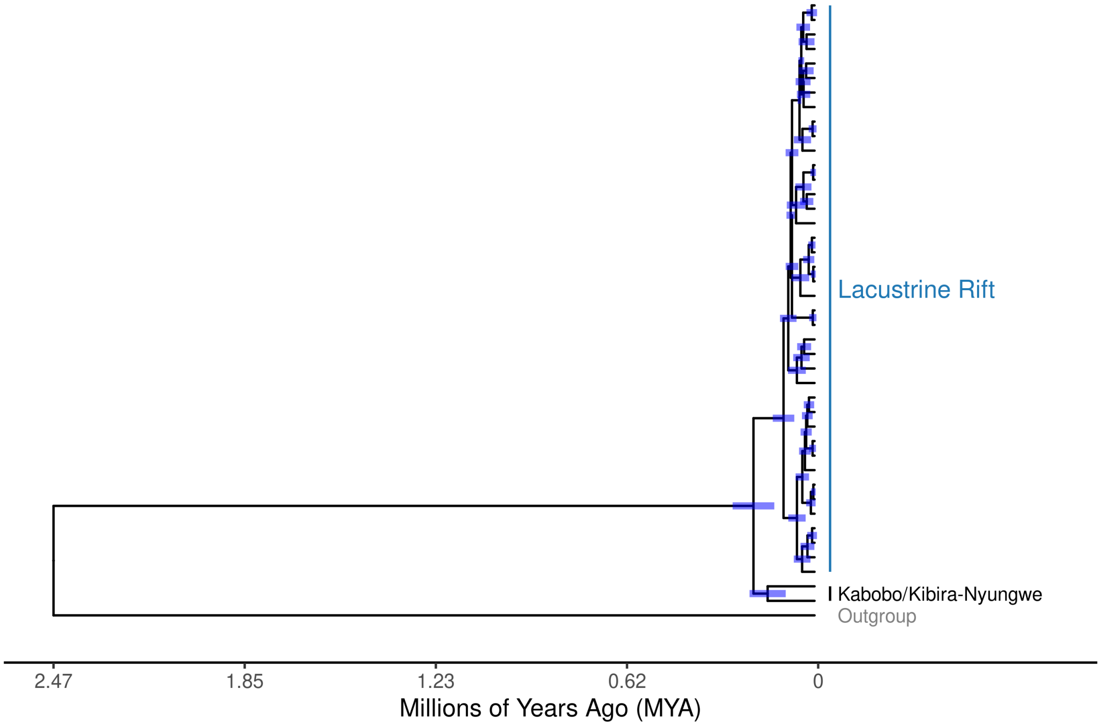

Figure C.14: *Sylvietta leucophrys* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Sylvietta whytii*. Note that the population *S. l. chapini* is not included in this study.

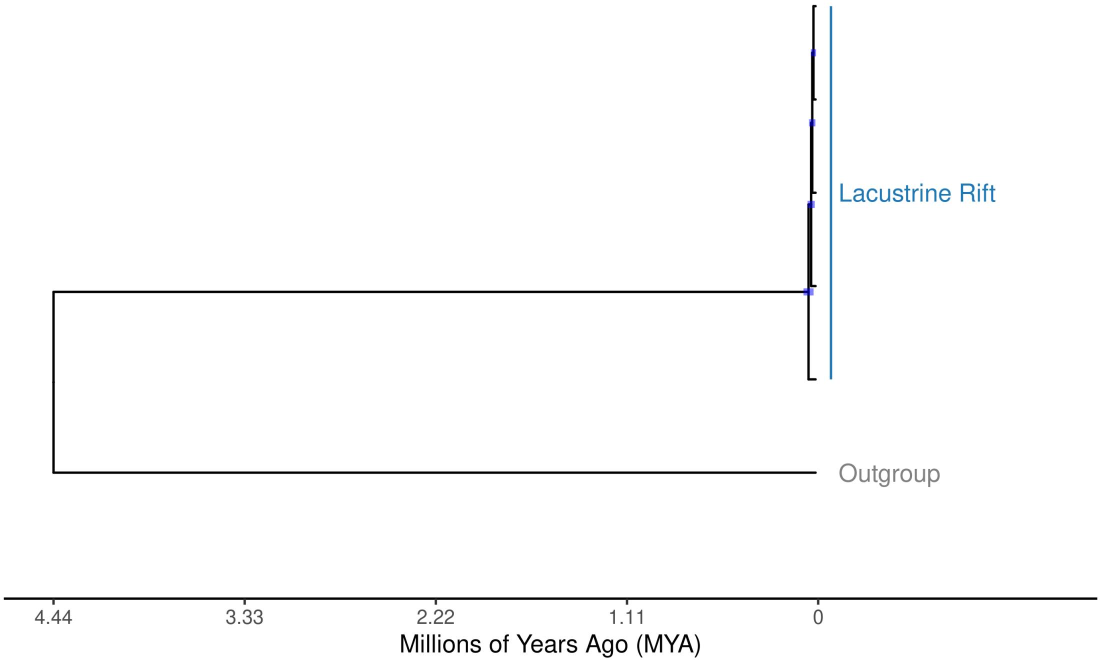

Figure C.15: *Graueria vittata* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Crithagra frontalis*.

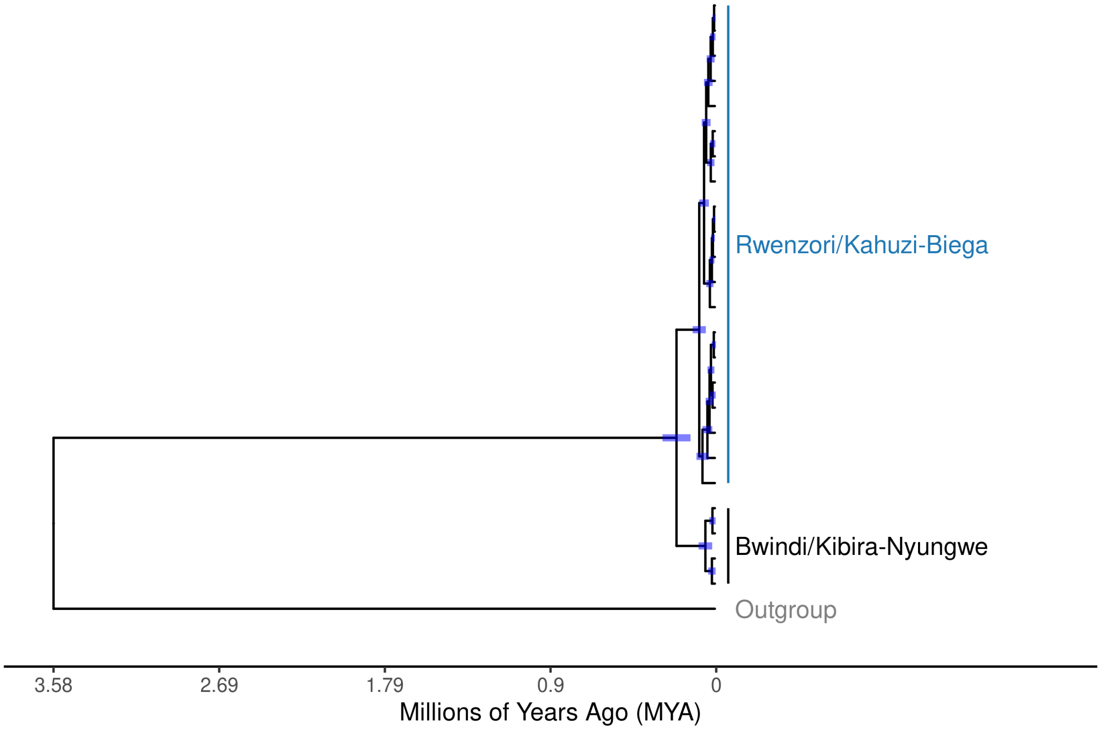

Figure C.16: *Oreolais ruwenzorii* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Camaroptera brevicaudata*.

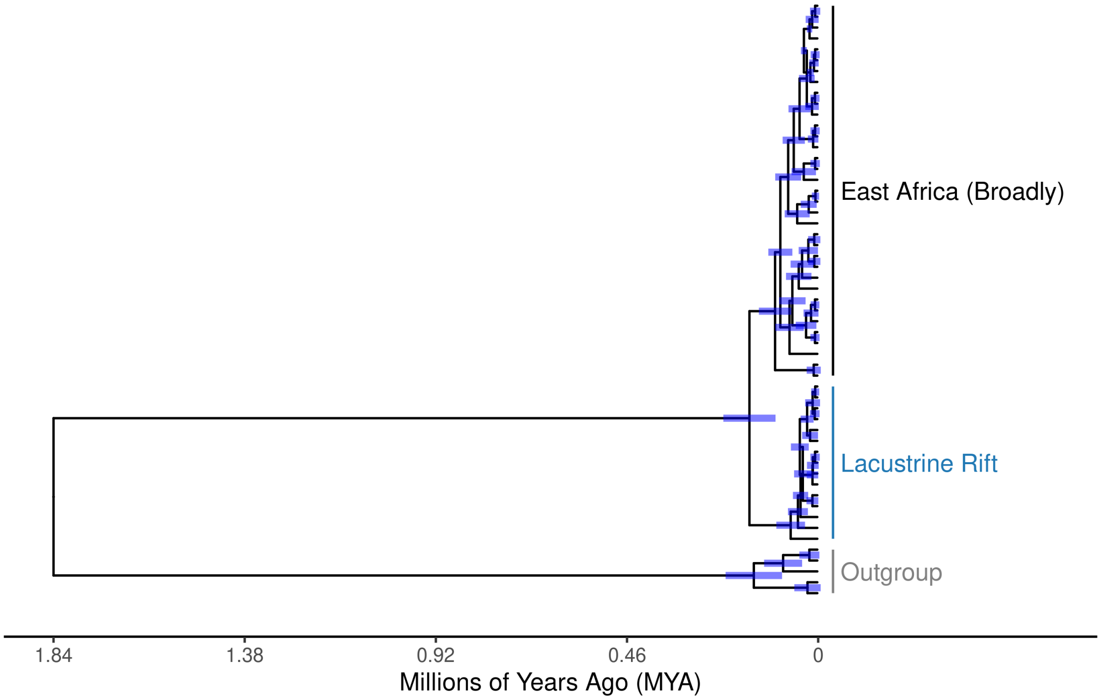

Figure C.17: *Iduna similis* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ND2 and ND3 genes. The outgroup is a clade of *Iduna natalensis*.

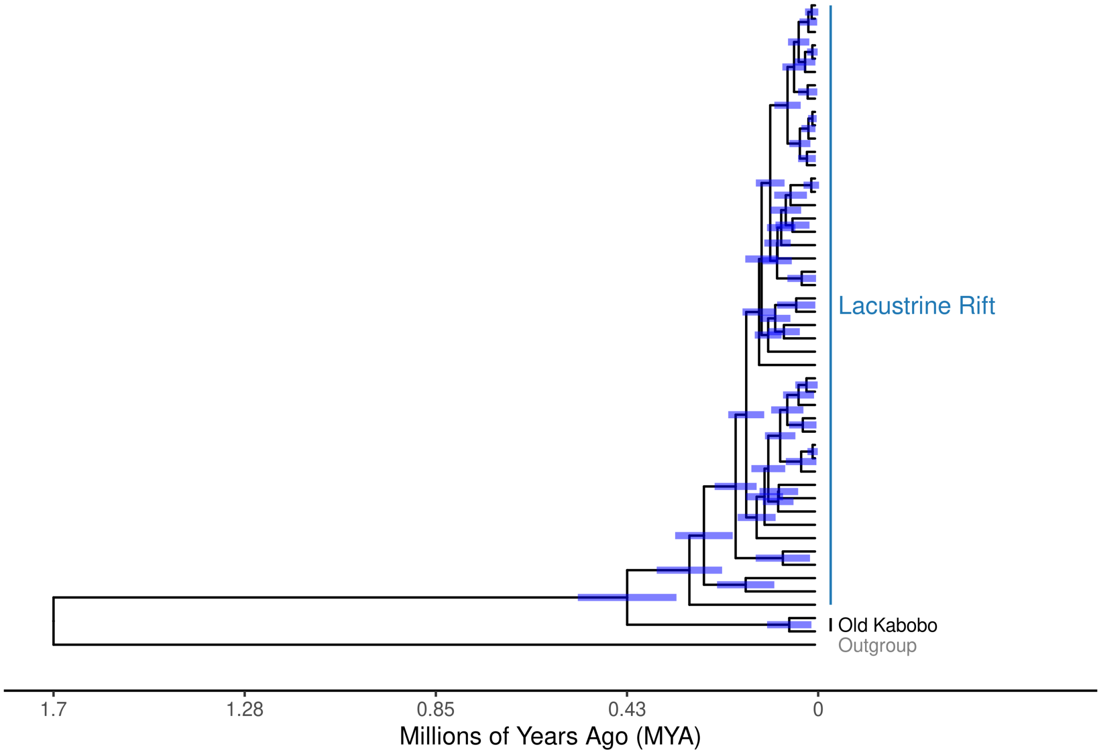

Figure C.18: *Phylloscopus laetus* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ND2 and ND3 genes. Note that individuals on Mt. Kabobo are described as a separate subspecies that the rest of the Lacustrine Rift (*P. l. schoutedeni*). The outgroup is *Phylloscopus umbrovirens*.

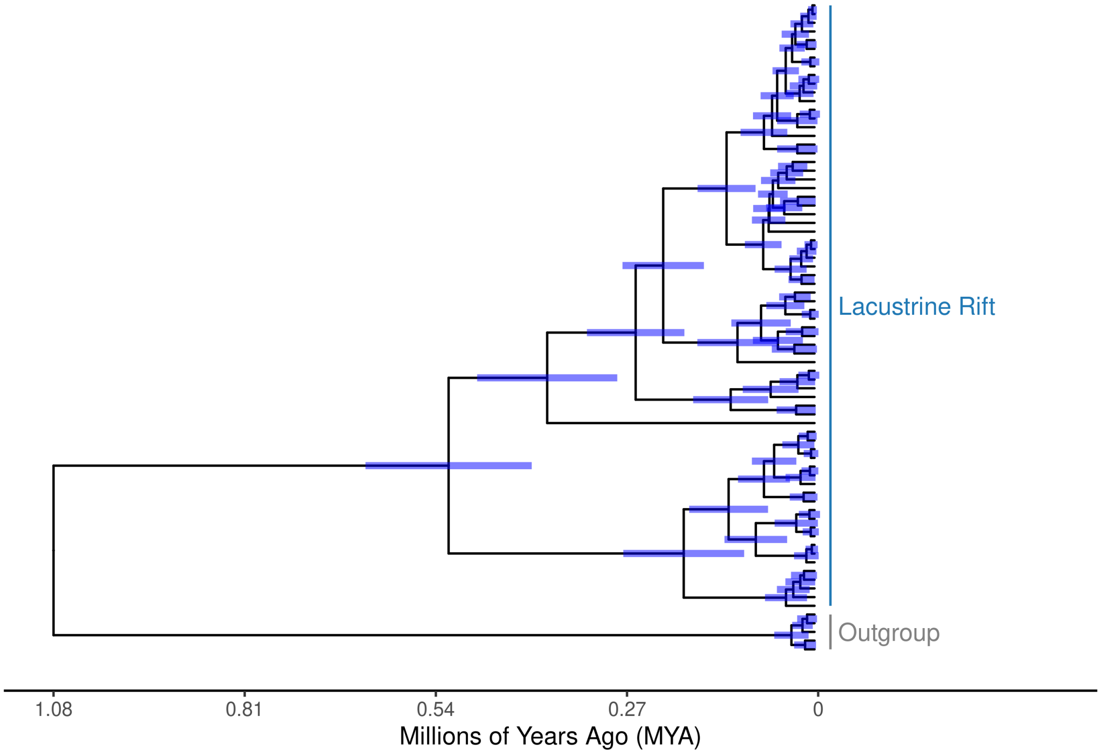

Figure C.19: *Sylvia atriceps* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6, ND2, and ND3 genes. Despite fairly deep divergences between haplotypes within *S. atriceps*, haplotypes are not restricted to individual geographic areas in the present day. The outgroup is a clade of *Sylvia abyssinica*.

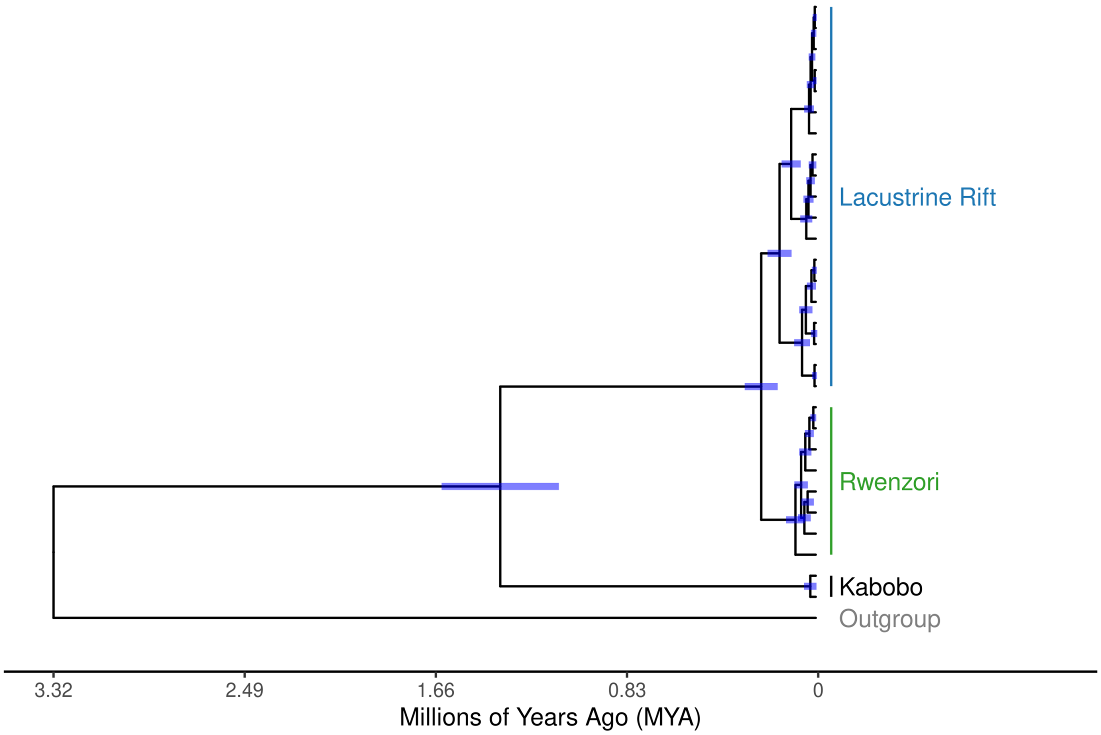

Figure C.20: *Cossypha archeri* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6, ND2, and ND3 genes. Note that we elevate the Mt. Kabobo population to species rank, *C. kimbutui*. The outgroup is *Cossyphicula roberti*.

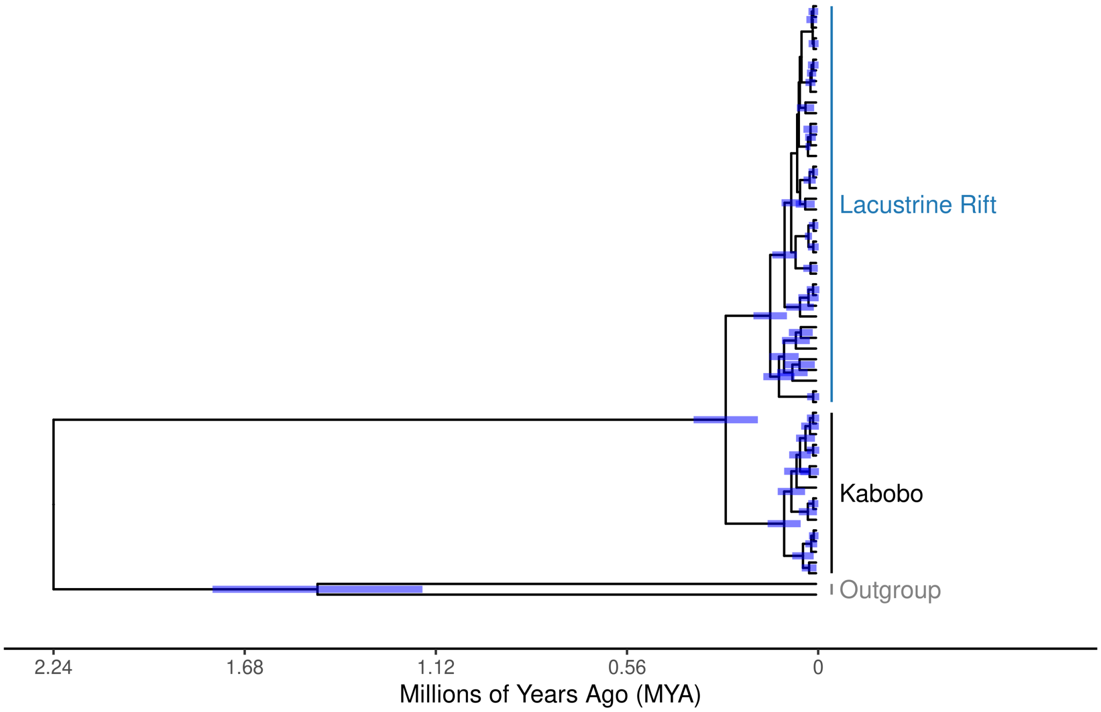

Figure C.21: *Chamaetylas poliophrys* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ND2 genes. Note that we elevate the Mt. Kabobo population to species rank (*C. kaboboensis*). The outgroup is a clade of *C. choloensis* and *C. fulleborni*.

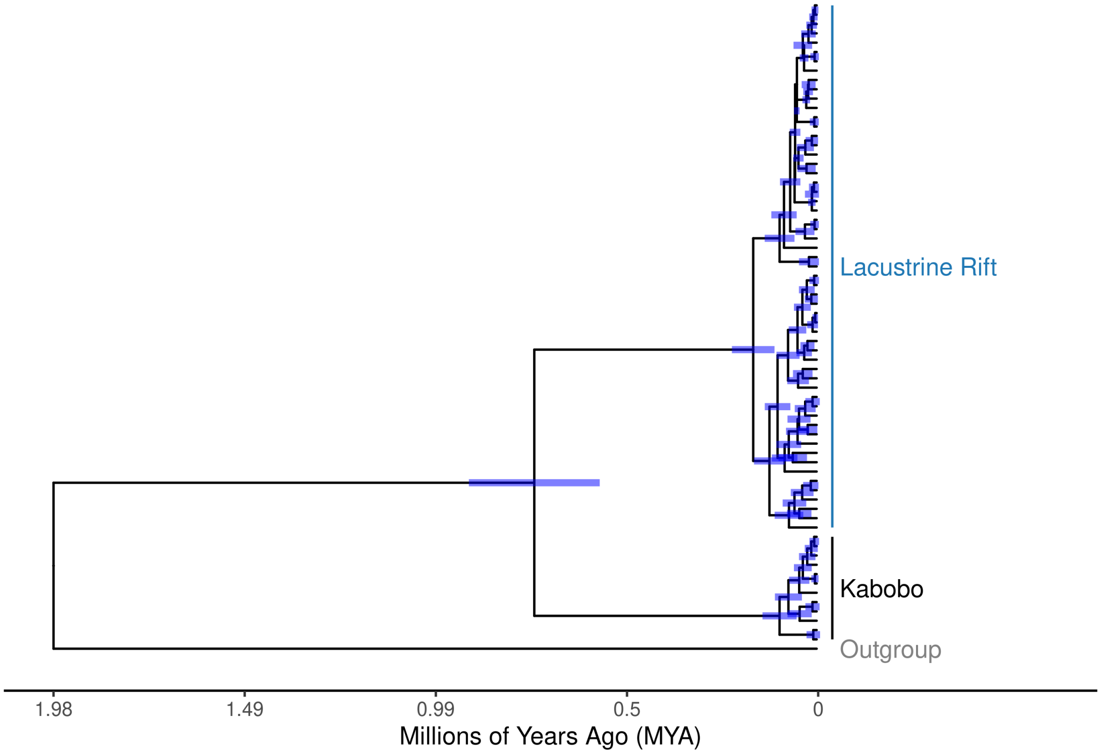

Figure C.22: *Cyanomitra alinae* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6 and ND2 genes. Note that we elevate the Mt. Kabobo population to species rank (*C. k. kaboboensis*, including the subspecies *marungensis*). The outgroup is *Cyanomitra verticalis*.

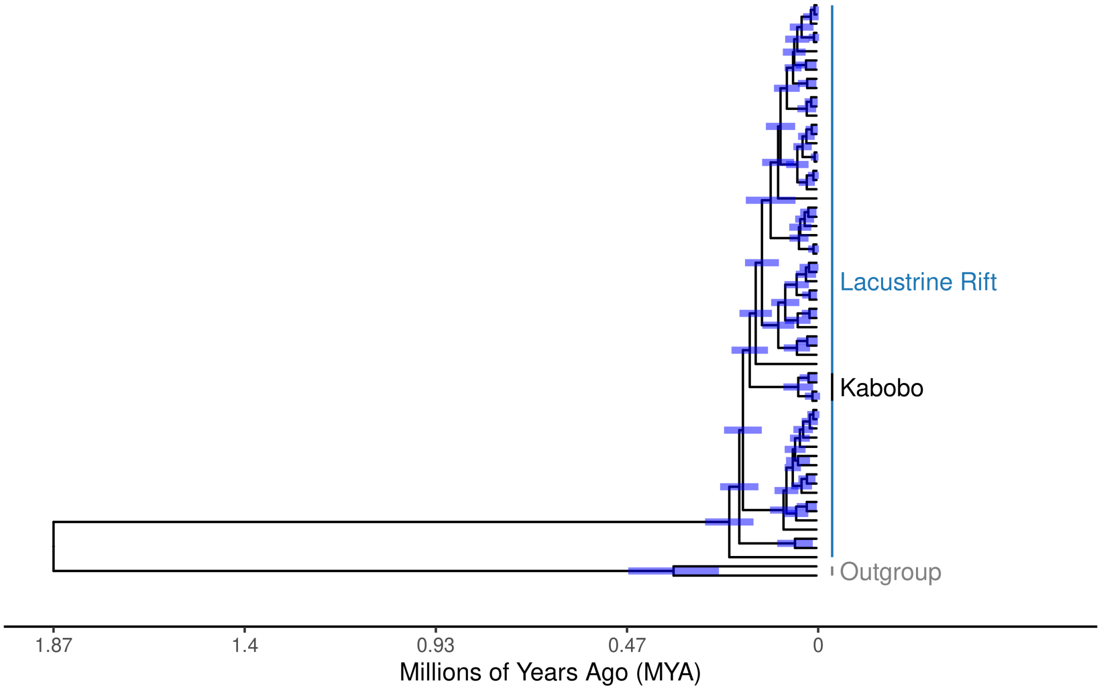

Figure C.23: *Cinnyris regius* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6 and ND2 genes. The outgroup is a pair of *C. reichenowi* and *C. preussi*.

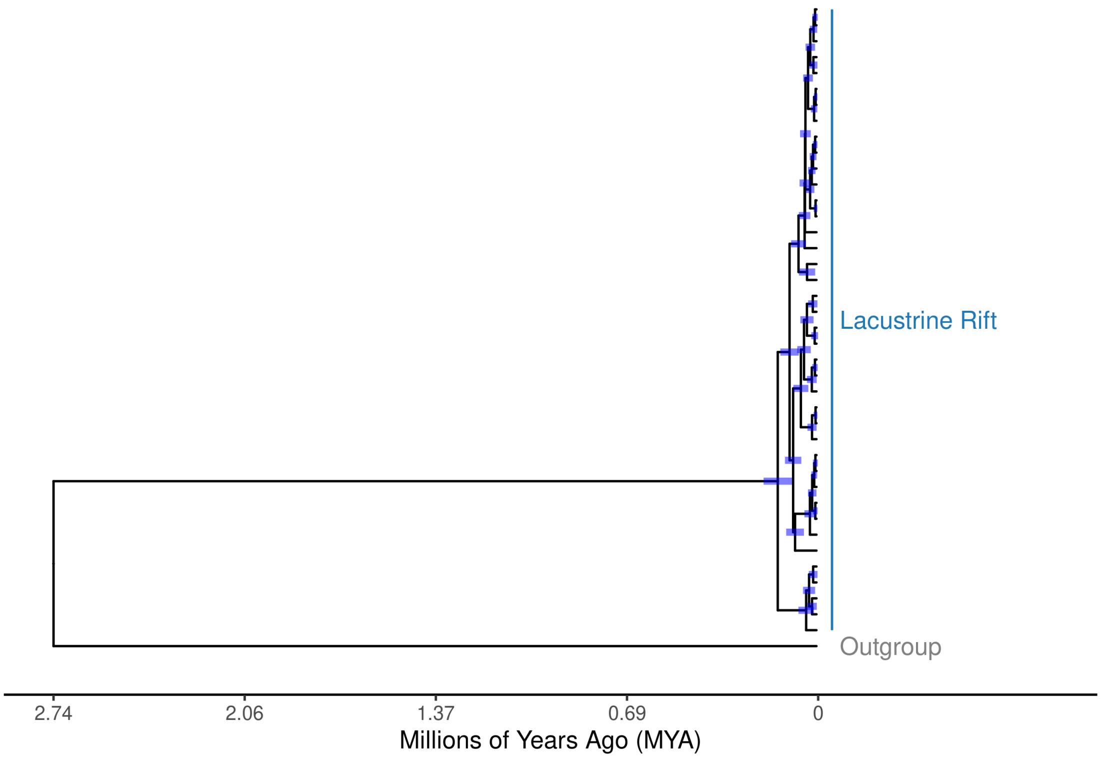

Figure C.24: *Ploceus alienus* time-calibrated phylogeny, with blue lines indicating the 95% confidence interval for divergence dates. Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Ploceus olivaceiceps*.

C.3.3 RAxML trees

The trees were created using RAxML.

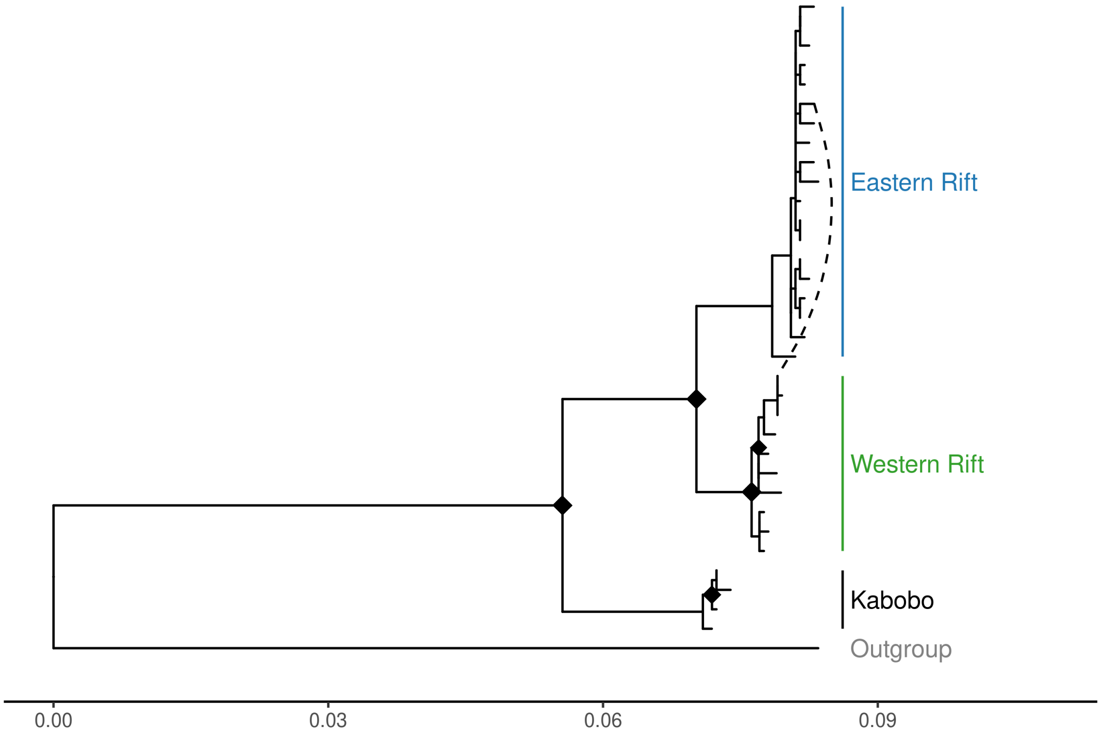

Figure C.25: *Batis diops* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Batis molitor*. Note that birds from Mt. Kabobo are not presently described as a separate subspecies from the rest of the Lacustrine Rift. The dashed line connects the Western Rift individual with an Eastern haplotype to an arbitrary eastern individual to illustrate the observed connectivity.

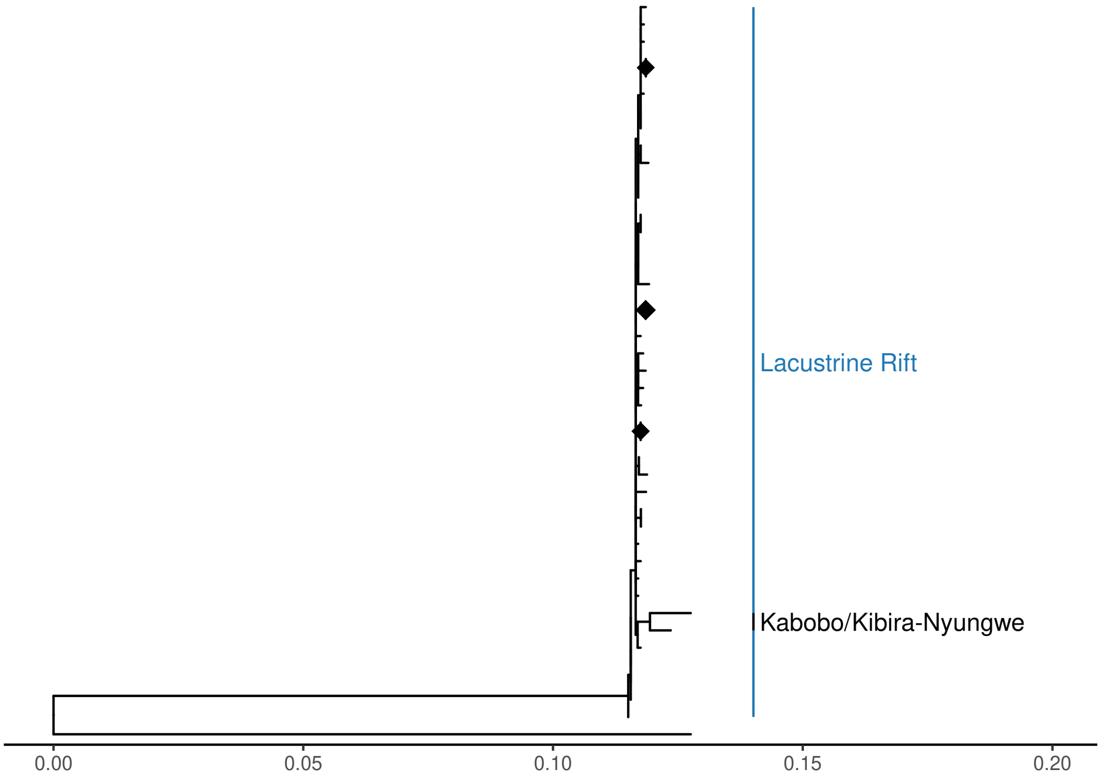

Figure C.26: *Sylvietta leucophrys* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Sylvietta whytii*. Note that the population *S. l. chapini* is not included in this study.

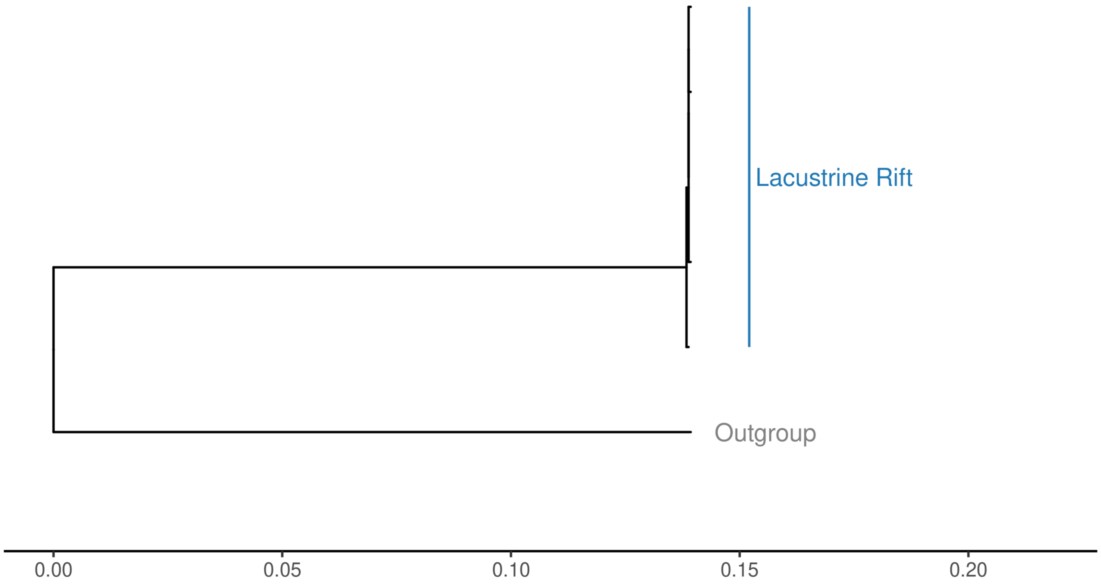

Figure C.27: *Graueria vittata* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Crithagra frontalis*.

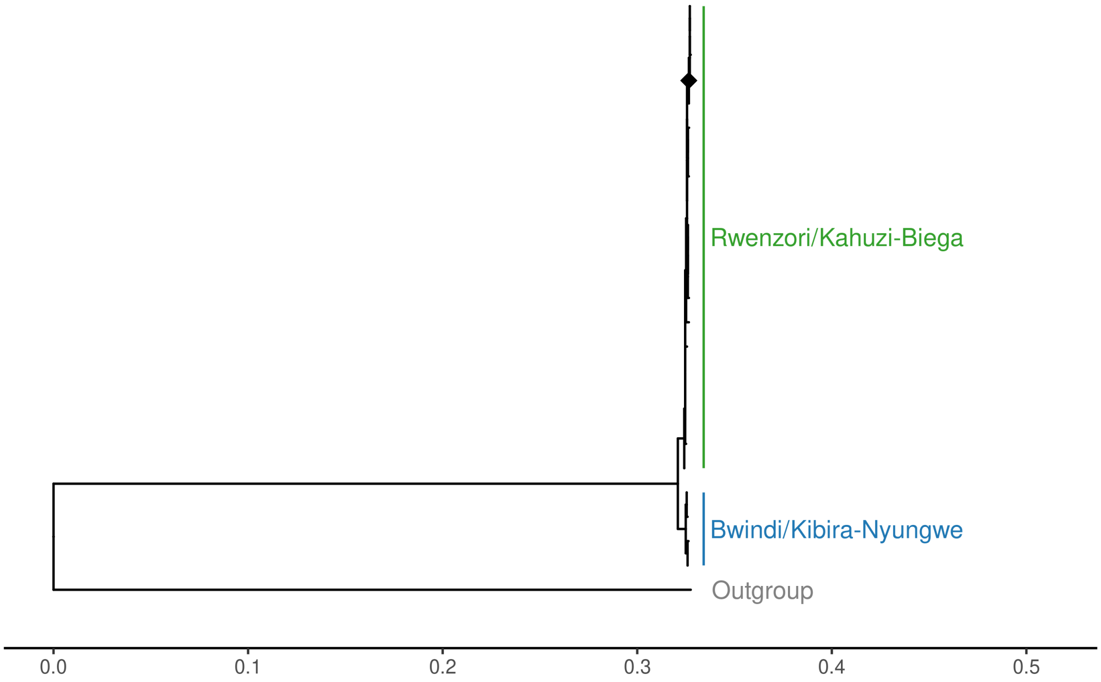

Figure C.28: *Oreolais ruwenzorii* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (i.e., large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Camaroptera brevicaudata*.

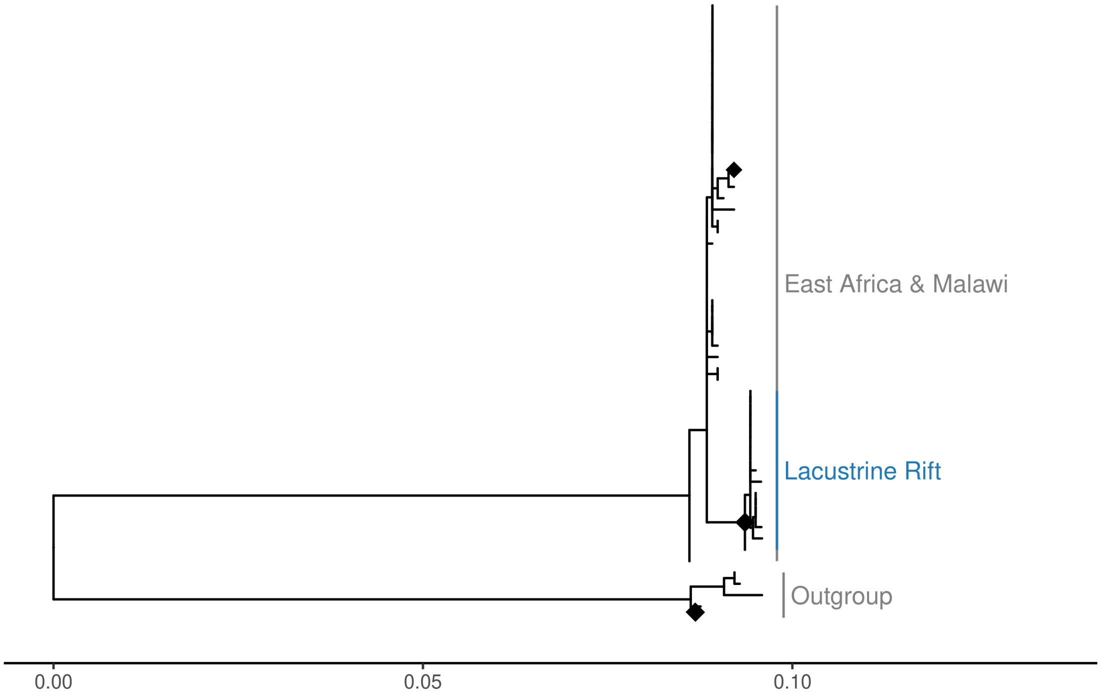

Figure C.29: *Iduna similis* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Iduna natalensis*.

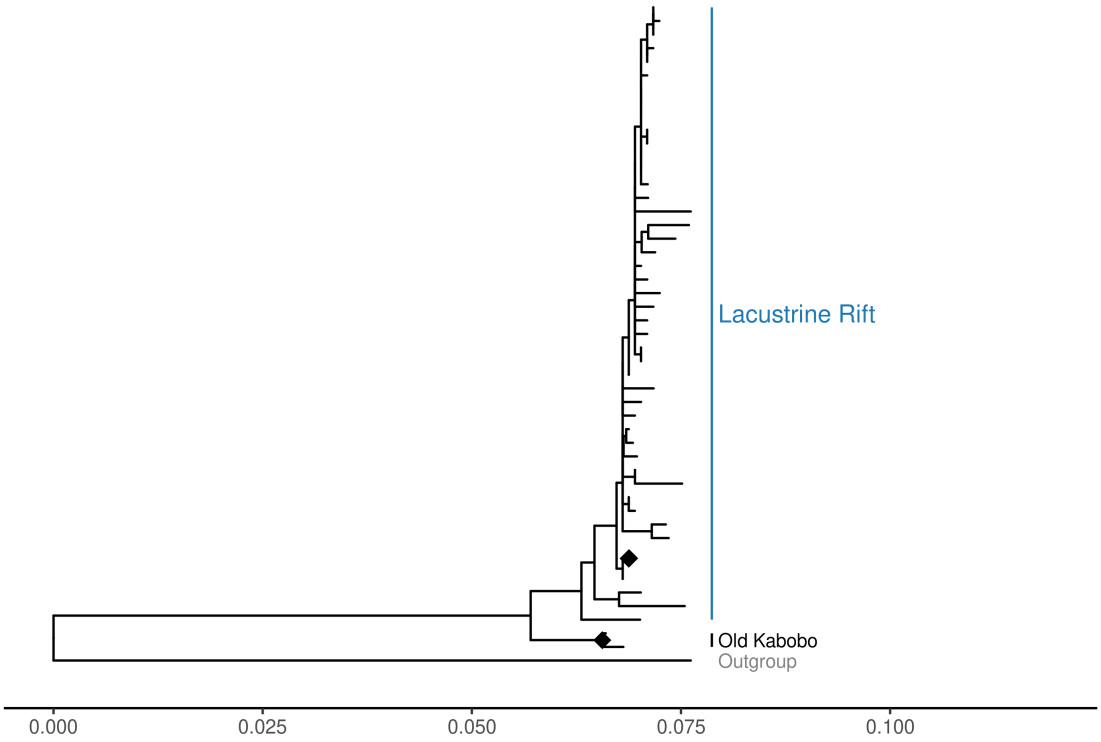

Figure C.30: *Phylloscopus laetus* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. Despite broadly co-occurring genetic lineages, the population on Mt. Kabobo has been described as its own subspecies (*schoutedeni*). The outgroup is *Phylloscopus umbrovirens*.

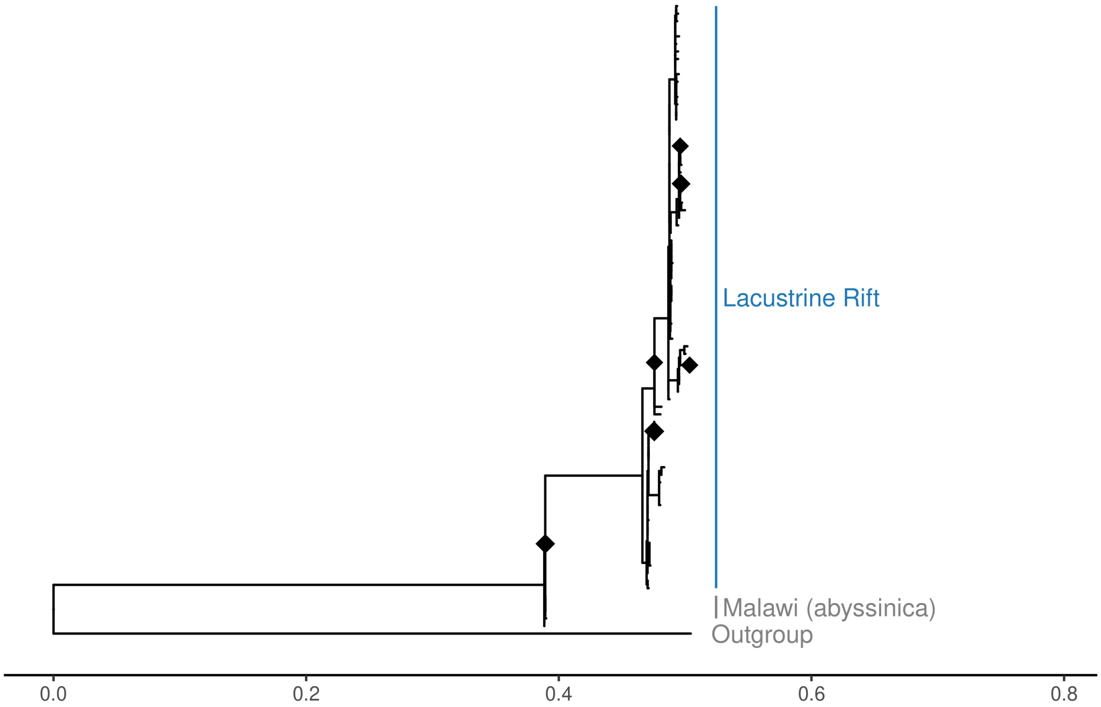

Figure C.31: *Sylvia atriceps* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ND2 and ND3 genes. Despite fairly deep divergences, all genetic groups are geographically intertwined. This tree includes individuals from *S. abyssinica* (denoted as 'Malawi' in the above plot) and has an outgroup of *Phylloscopus laetus*.

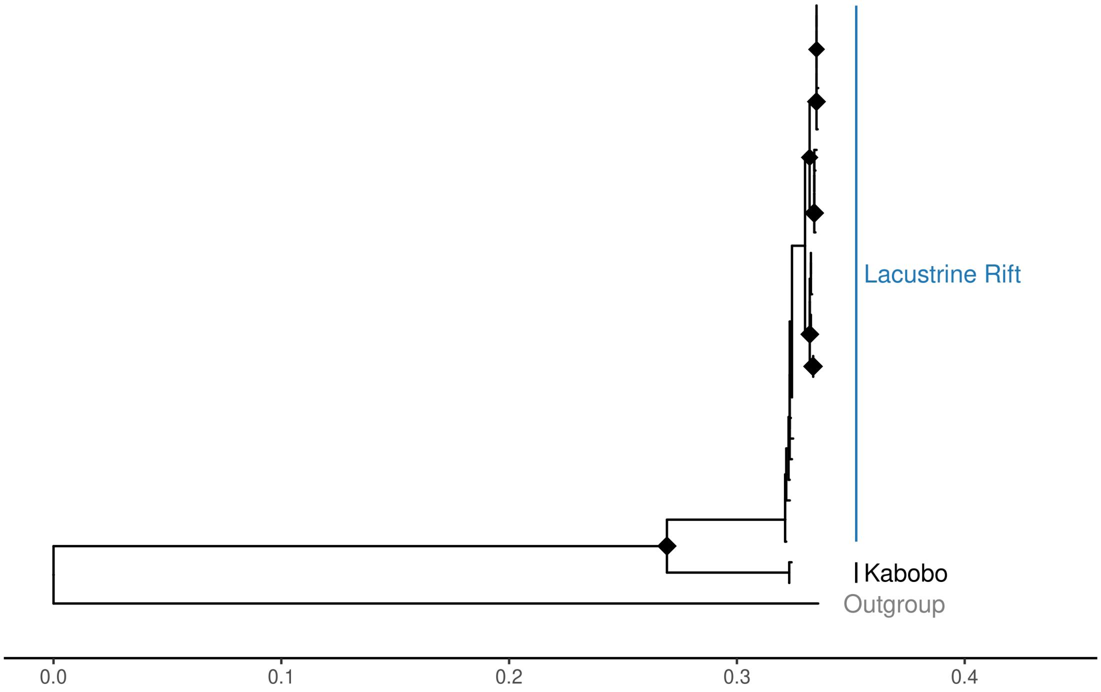

Figure C.32: *Cossypha archeri* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. Note that two major clades are apparent with high support, which we split as two species (*C. archeri* and *C. kimbutui*). The outgroup is *Cossyphicula roberti*.

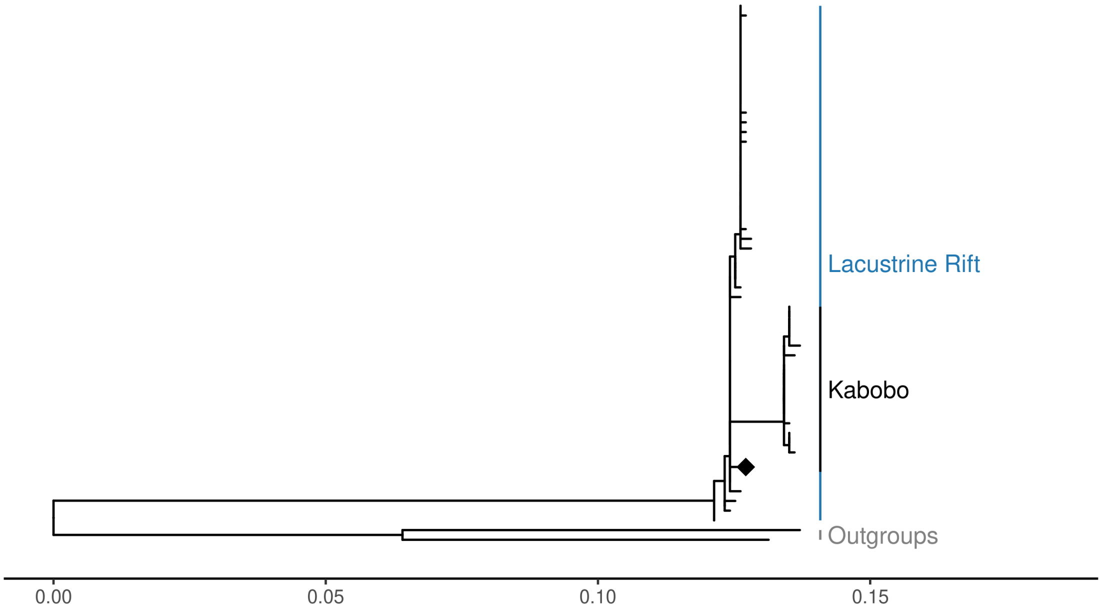

Figure C.33: *Chamaetylas poliophrys RaxML* phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ND2 genes. We separate birds from Mt. Kabobo (*C. kaboboensis*) as a separate species. The outgroups are *C. choloensis* and *C. fulleborni*.

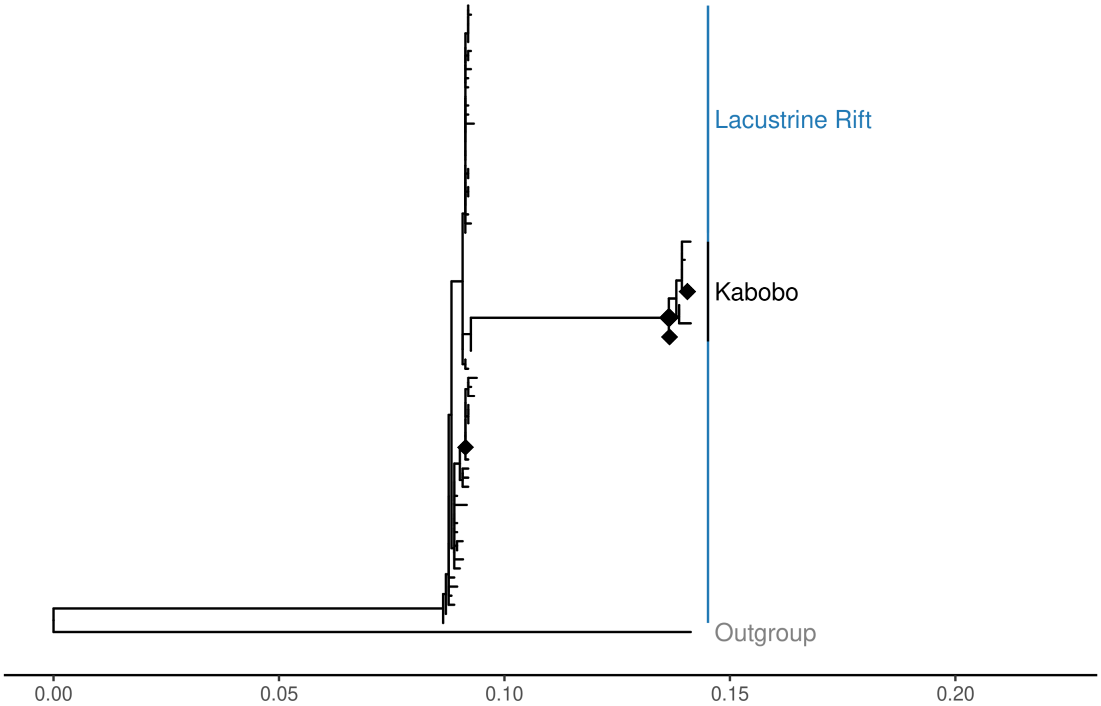

Figure C.34: *Cyanomitra alinae* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6 and ND2 genes. Note that we elevate the Mt. Kabobo population to species level (*C. k. kaboboensis*, including the adjacent *C. k. marungensis*). The outgroup is *Cyanomitra verticalis*.

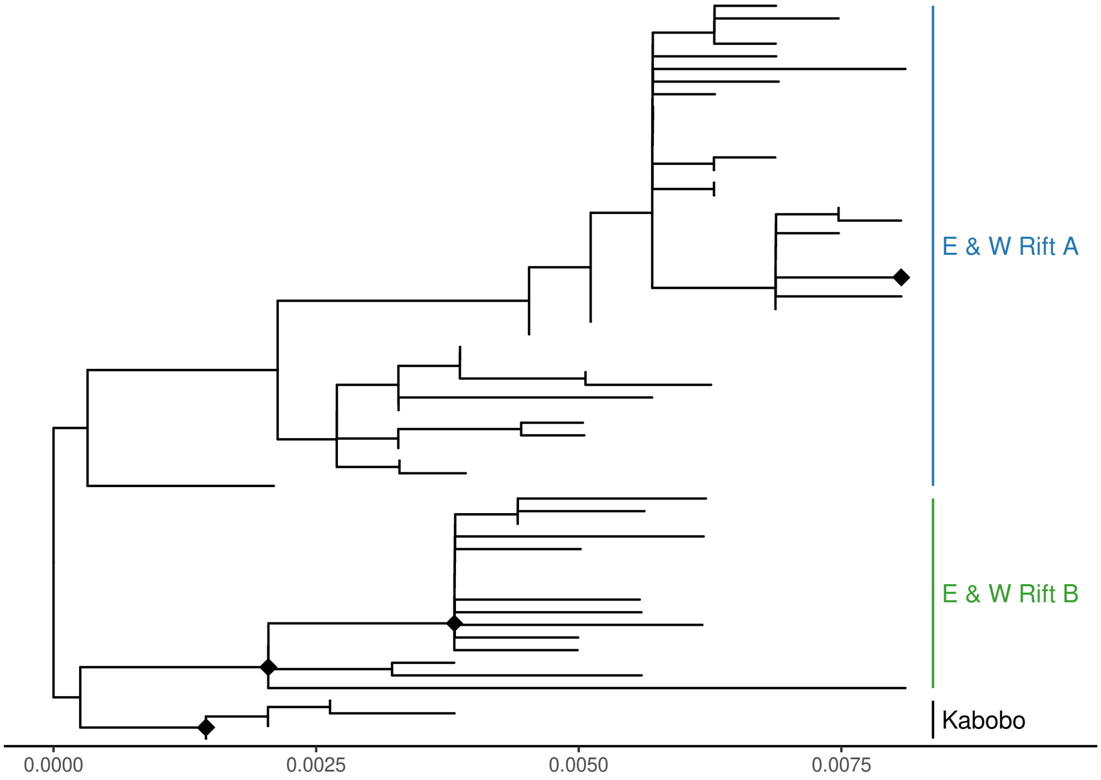

Figure C.35: *Cinnyris regius* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, -Fib5, and TGF- 2 genes. No outgroup is provided for this tree as no other sunbird was sequenced with the exact same genetic markers; some groups do have 100% support (*e.g.*, Kabobo), similar to the haplotype analysis.

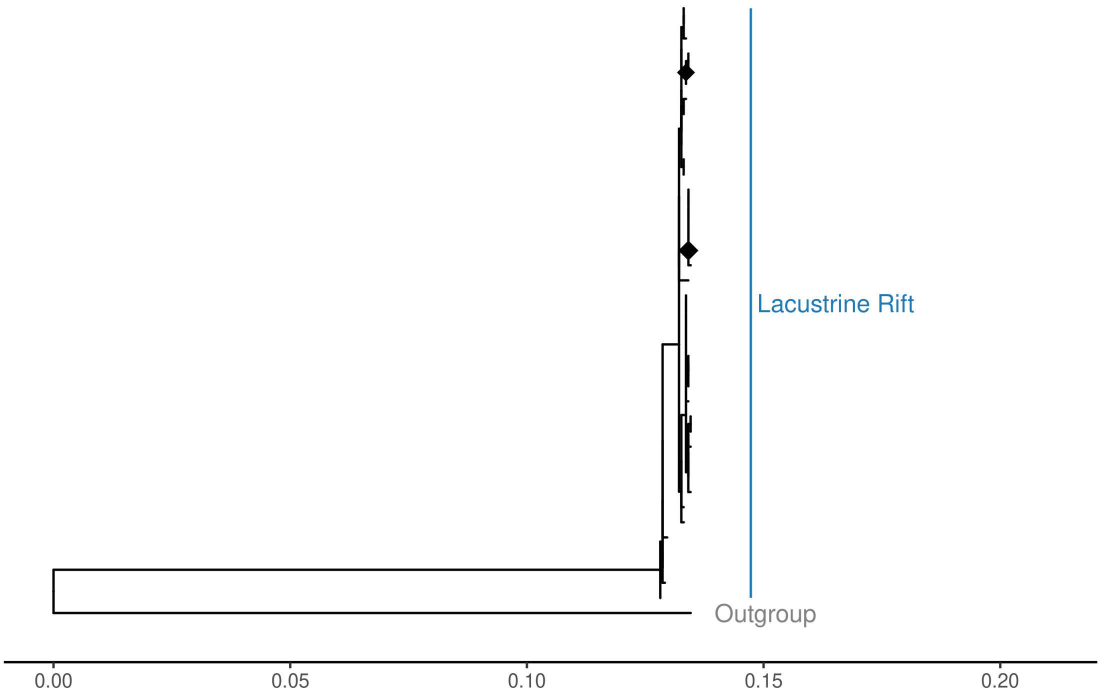

Figure C.36: *Ploceus alienus* **RaxML** phylogeny, rooted at the midpoint and with nodes sized relative to support (*i.e.*, large nodes 100%, nodes <75% generally not visible). Tree utilizes ATP6, ND2, and ND3 genes. The outgroup is *Ploceus olivaceiceps*.

C.4 Distribution models

C.4.1 Random Forests

The following are distribution models created via Random Forests.

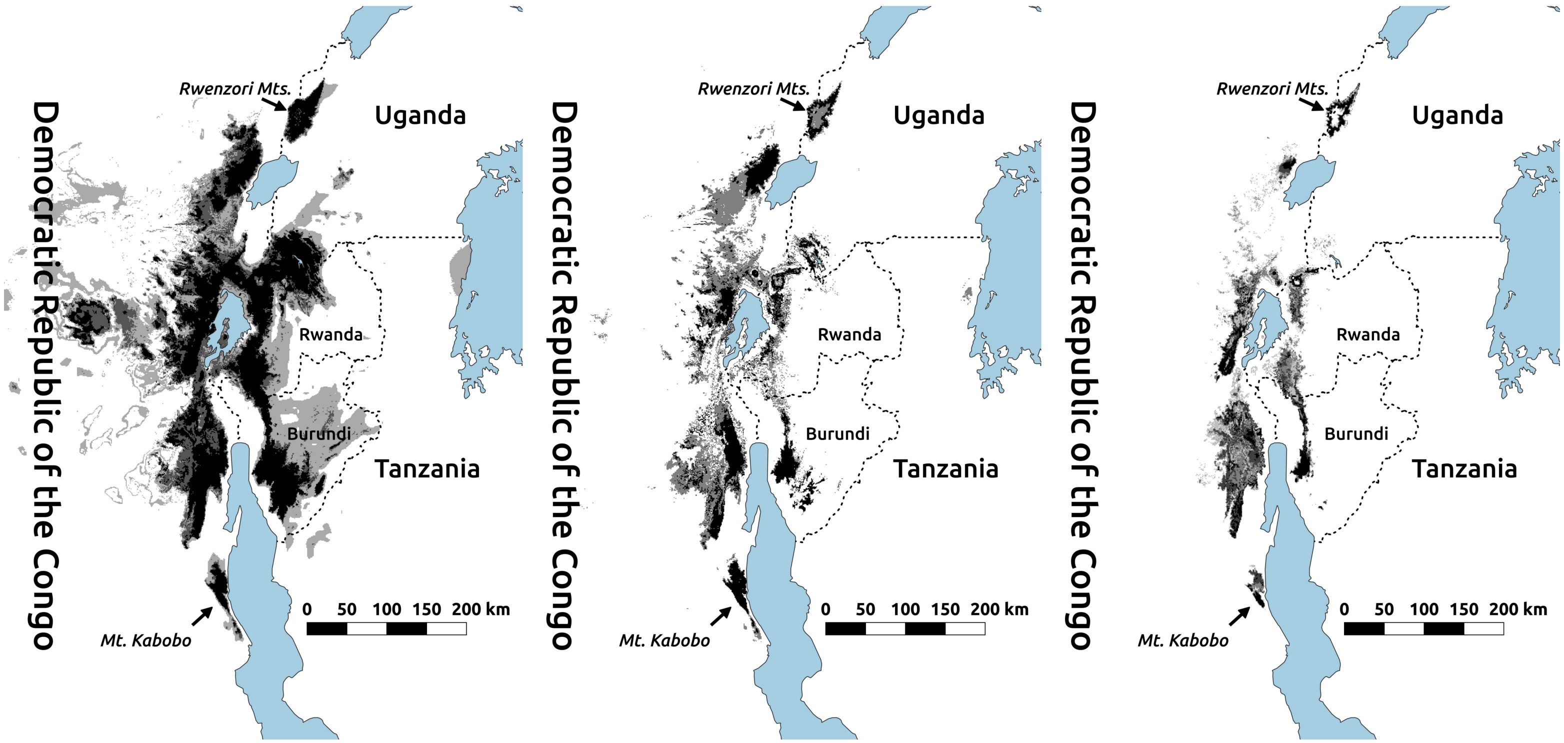

Figure C.37: *Batis diops*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

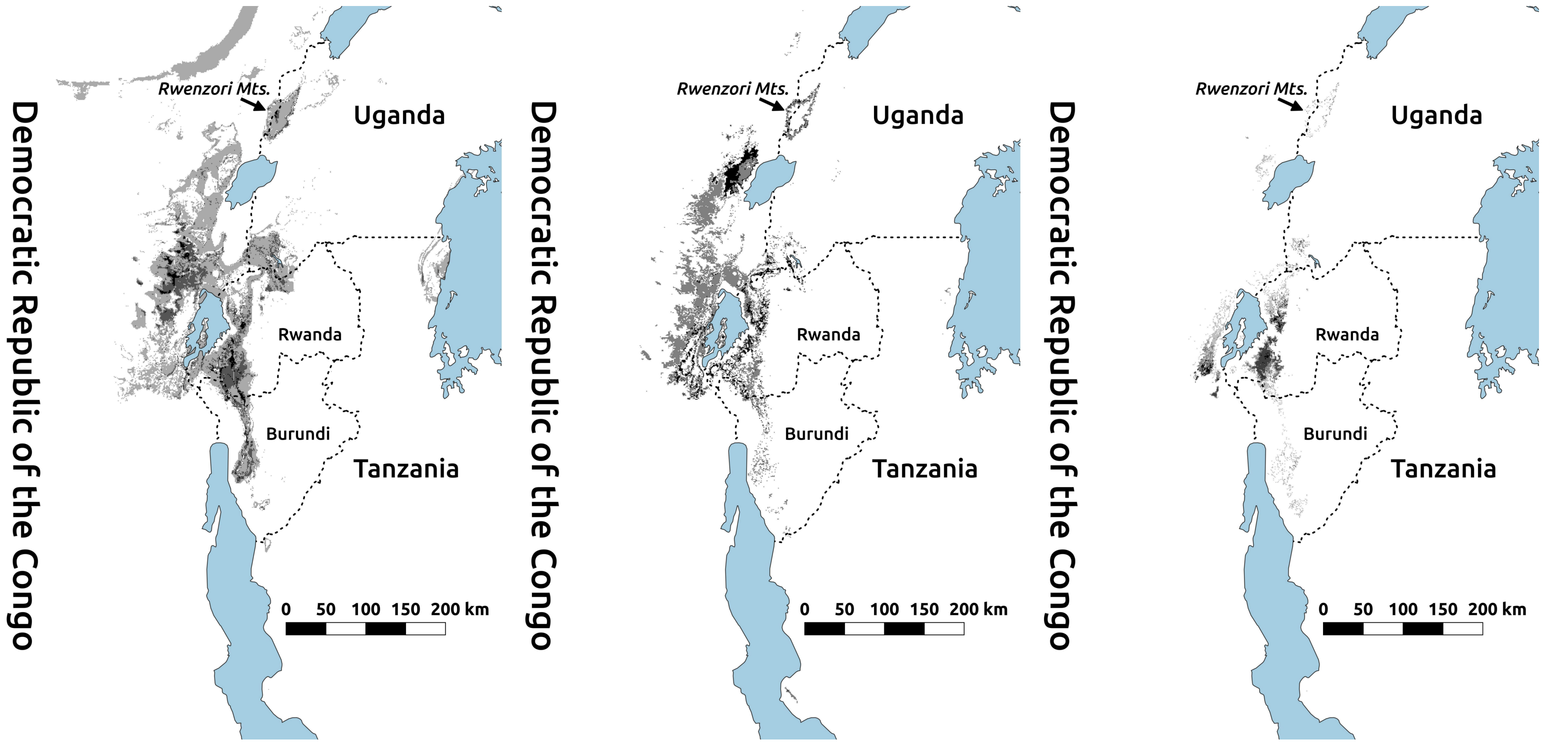

Figure C.38: *Sylvietta leucophrys.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

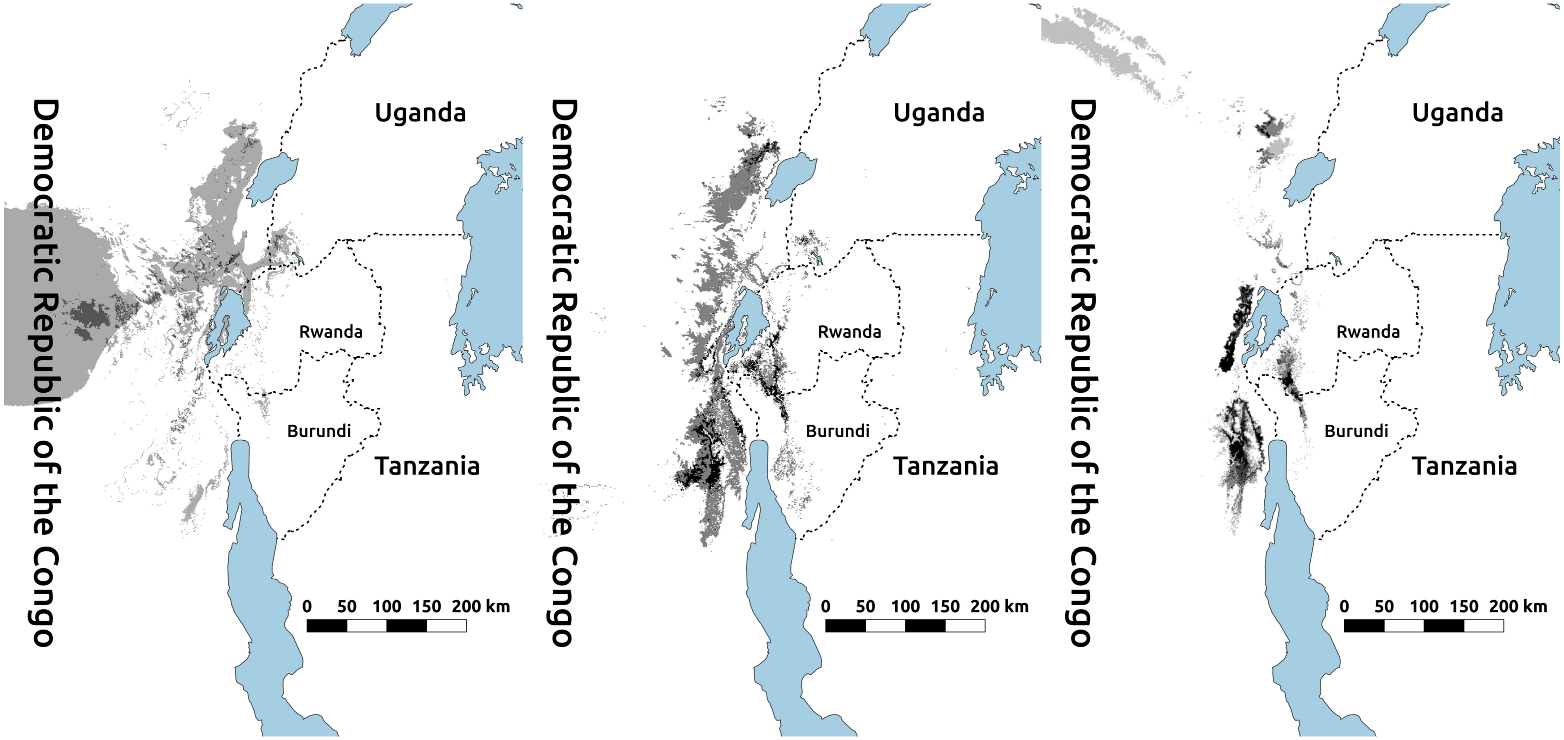

Figure C.39: *Graueria vittata.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

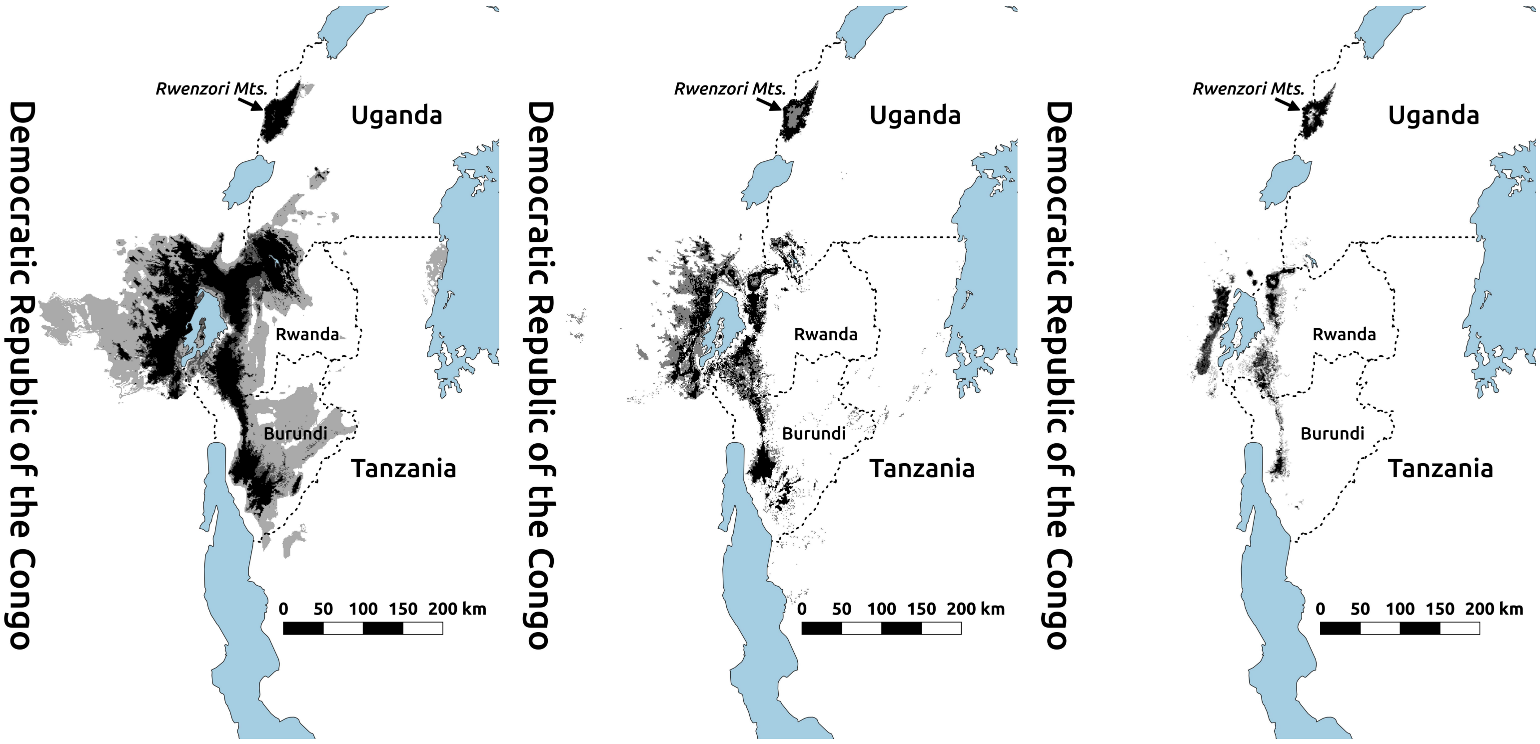

Figure C.40: *Oreolais ruwenzorii.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

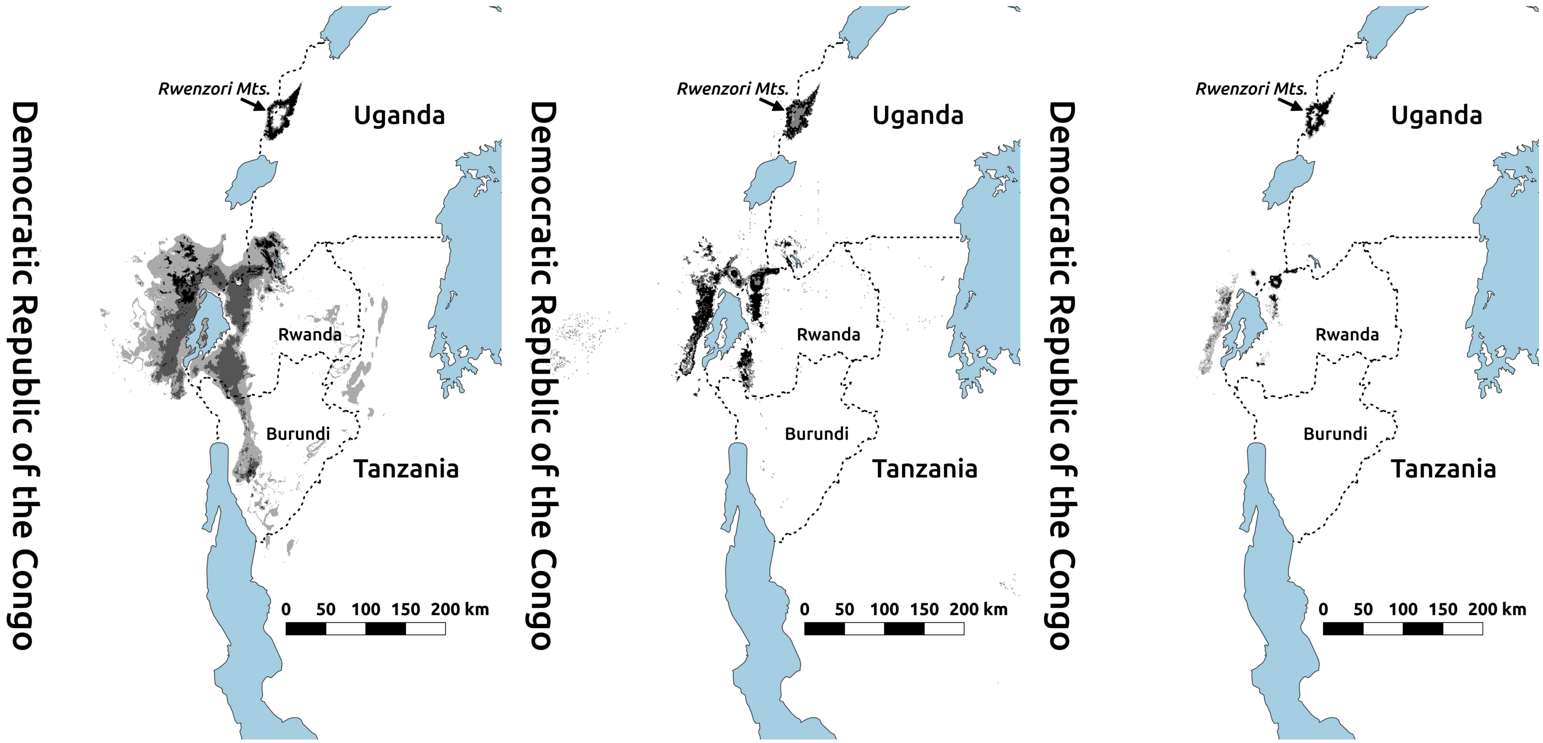

Figure C.41: *Iduna similis.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

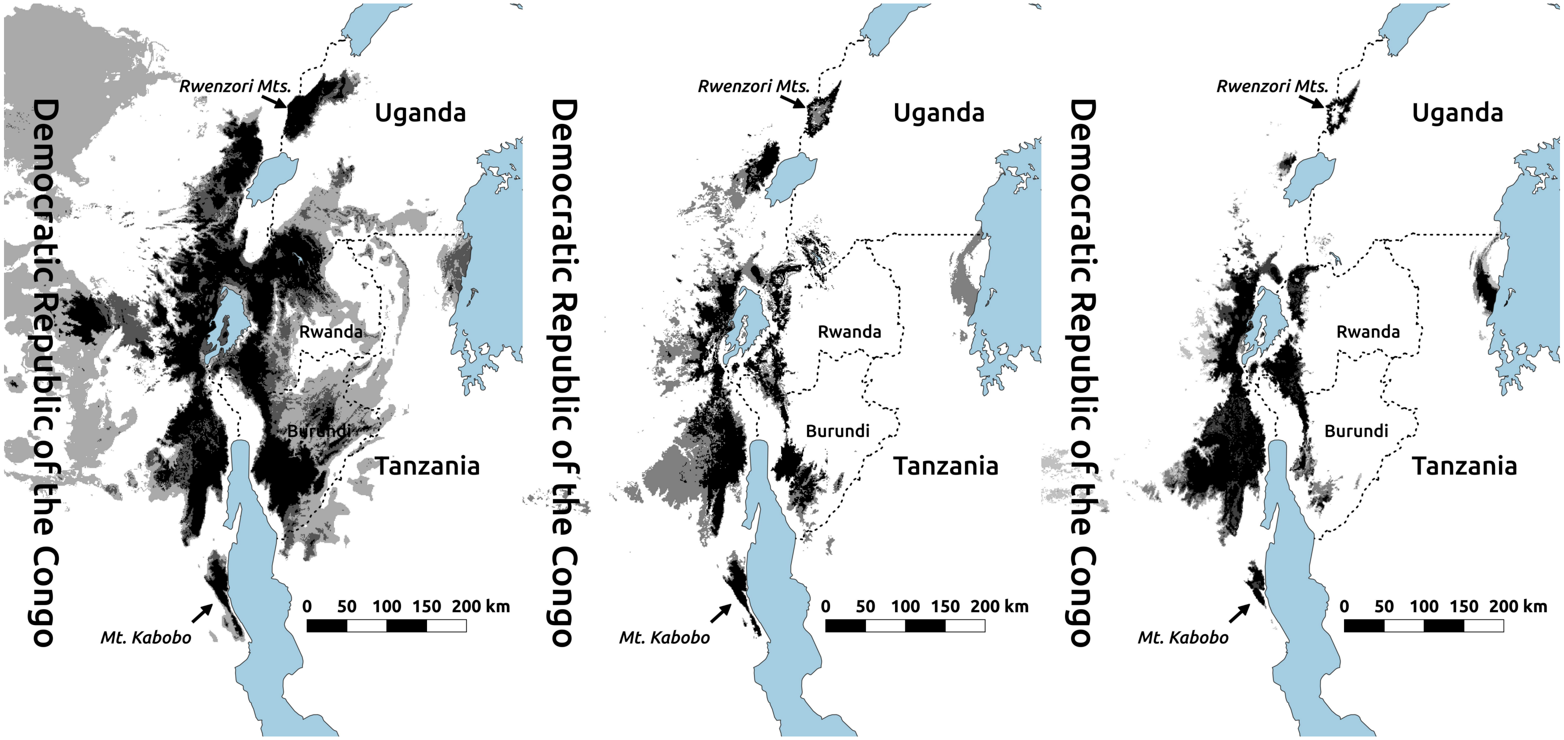

Figure C.42: *Phylloscopus laetus*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

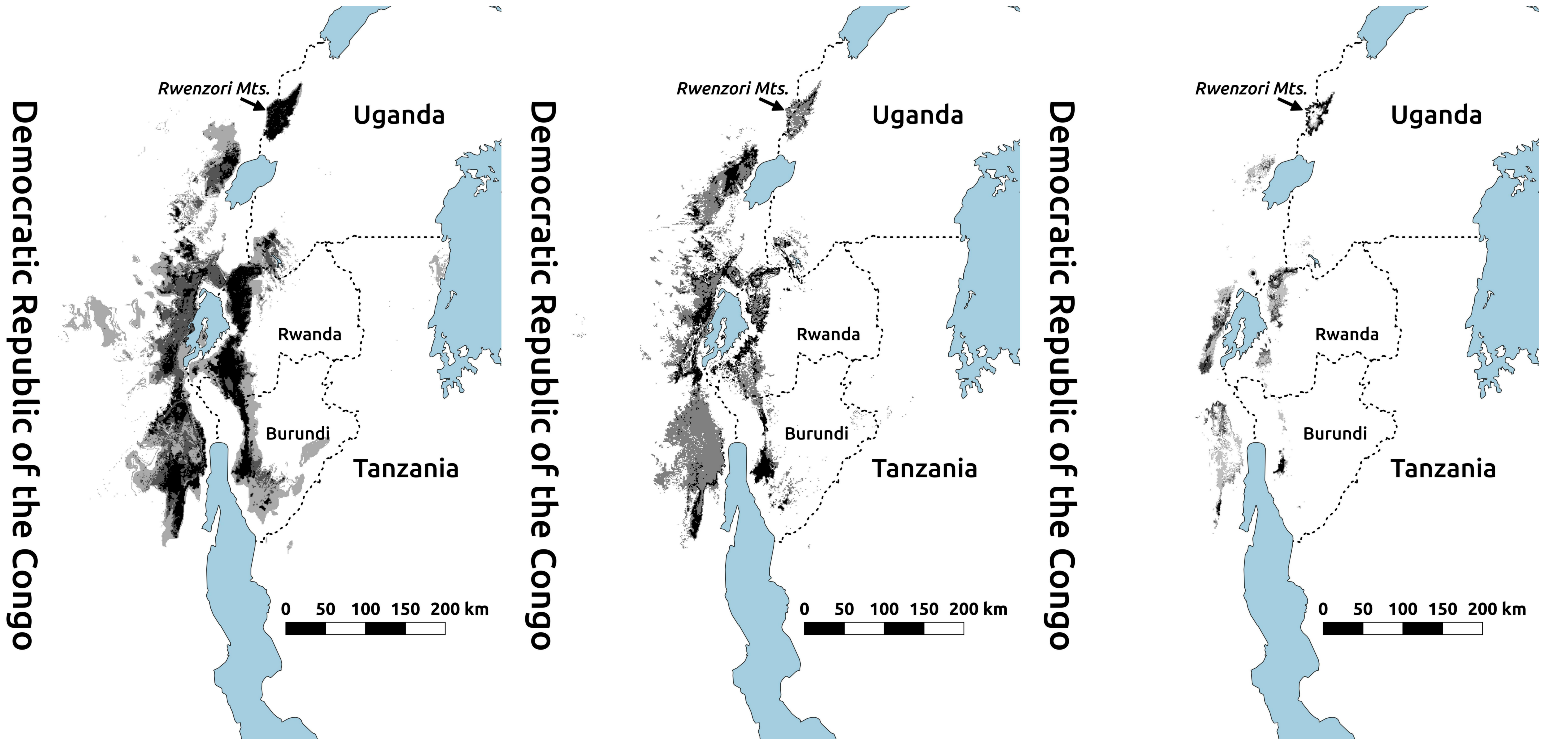

Figure C.43: *Sylvia atriceps*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

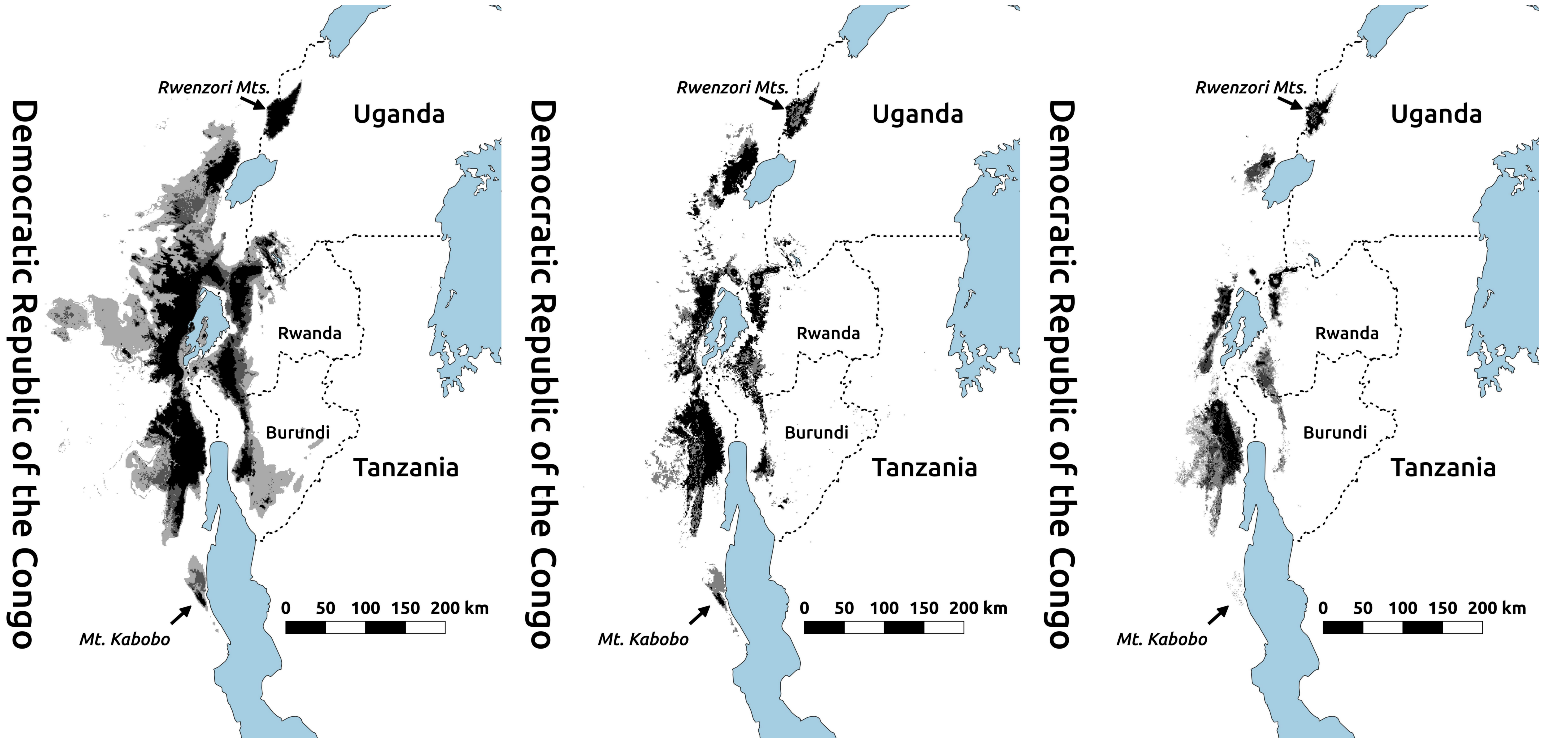

Figure C.44: *Cossypha archeri.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

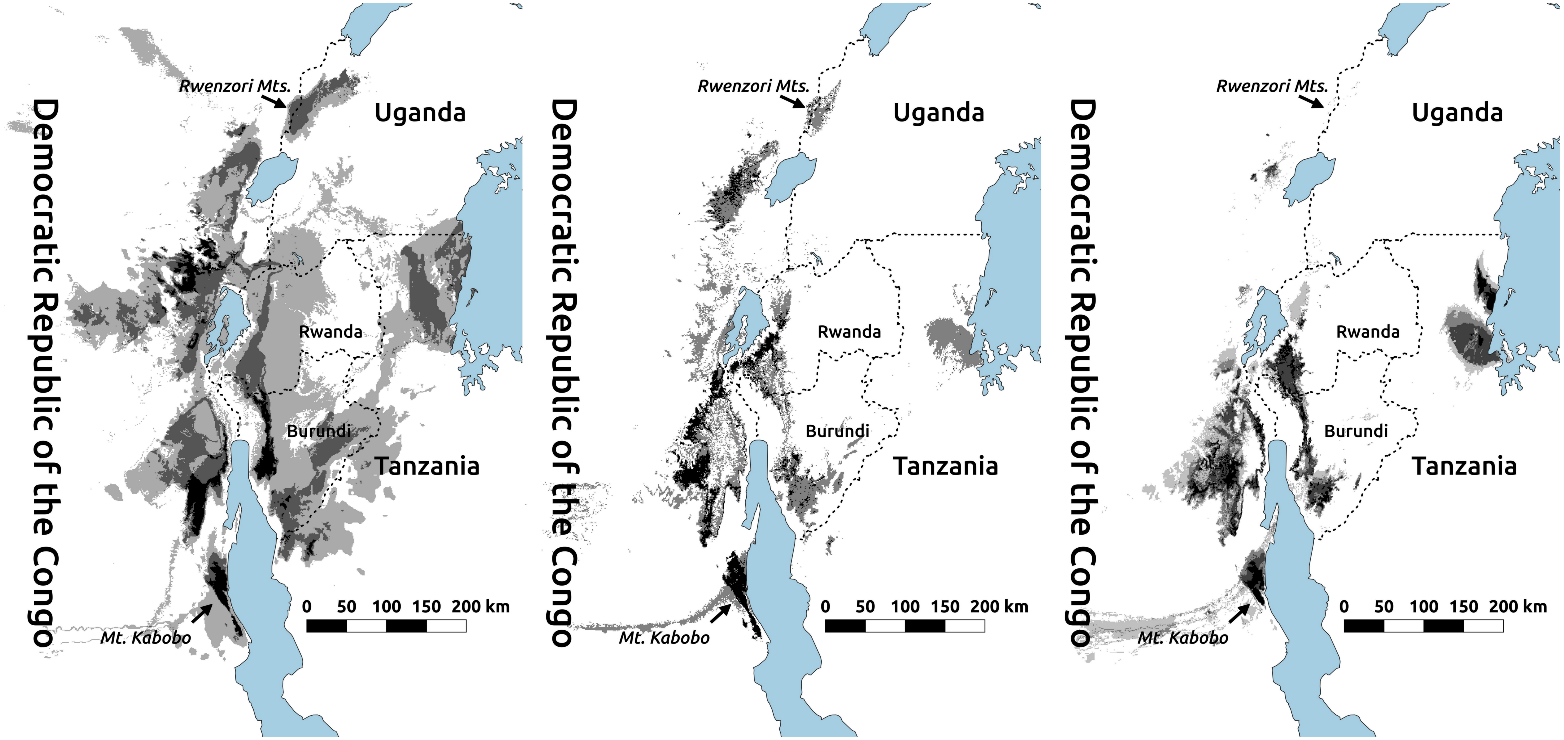

Figure C.45: *Chamaetylas poliophrys*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

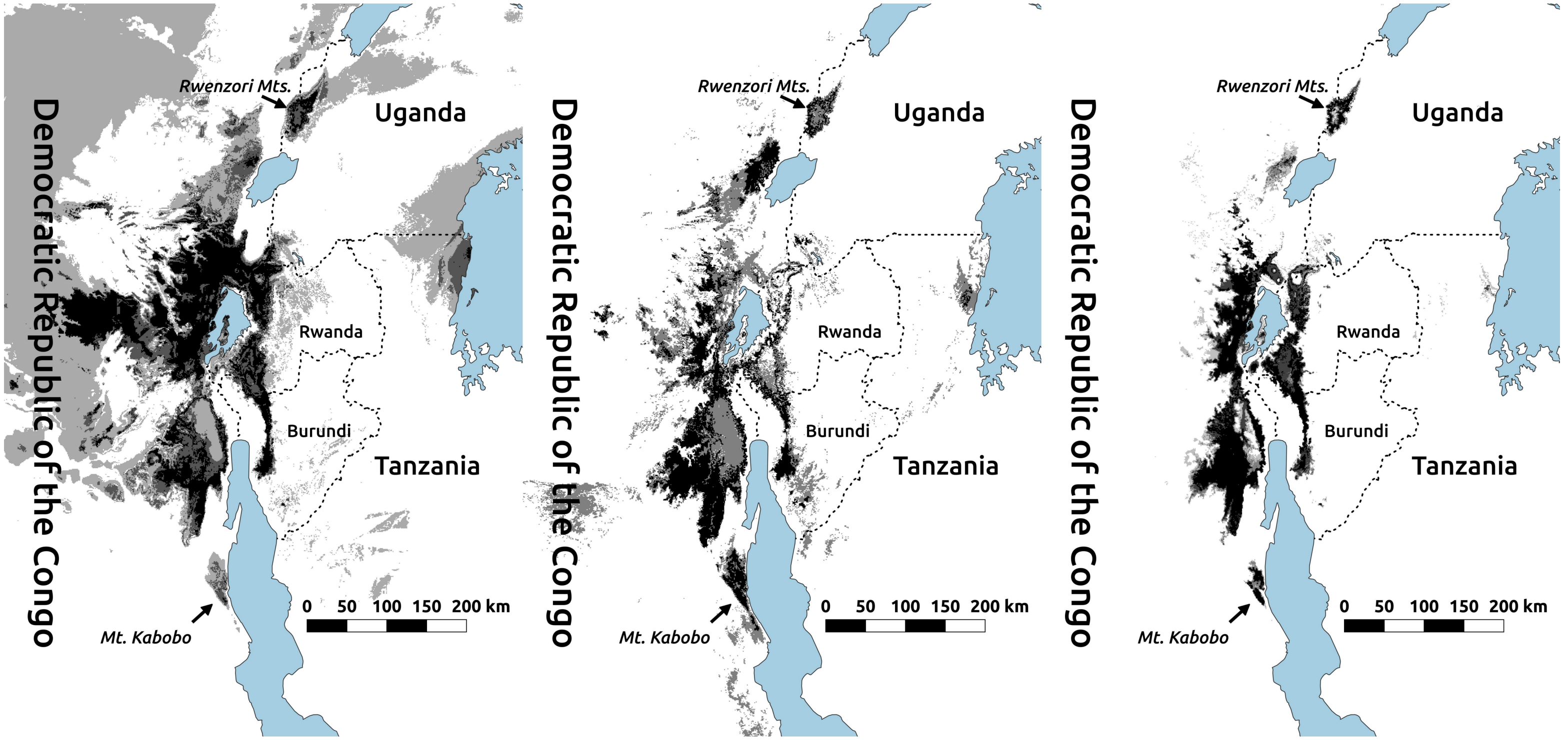

Figure C.46: *Cyanomitra alinae.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

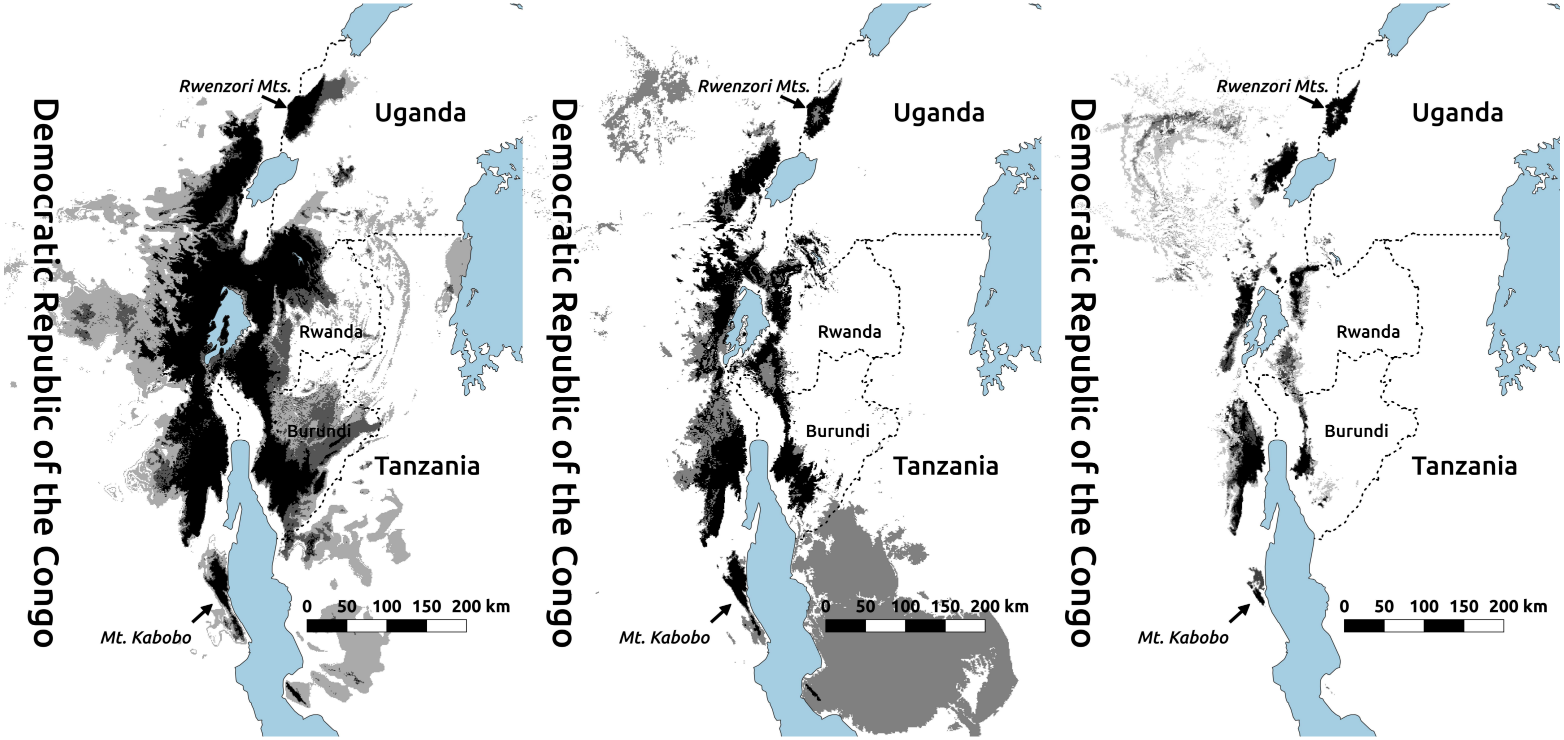

Figure C.47: *Cinnyris regius*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

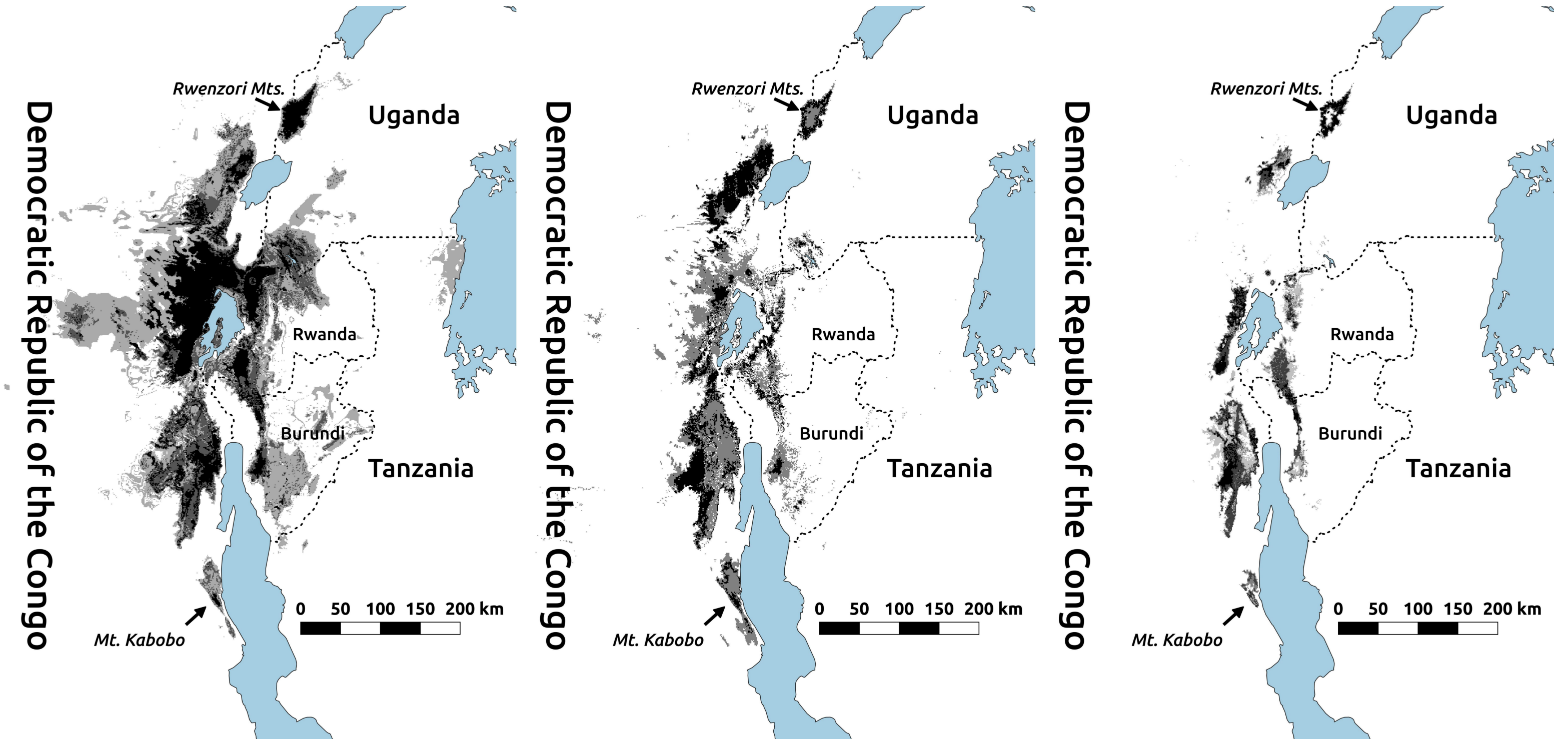

Figure C.48: *Ploceus alienus*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

C.4.2 Minimum volume ellipsoids

The following models were created using minimum volume ellipsoids.

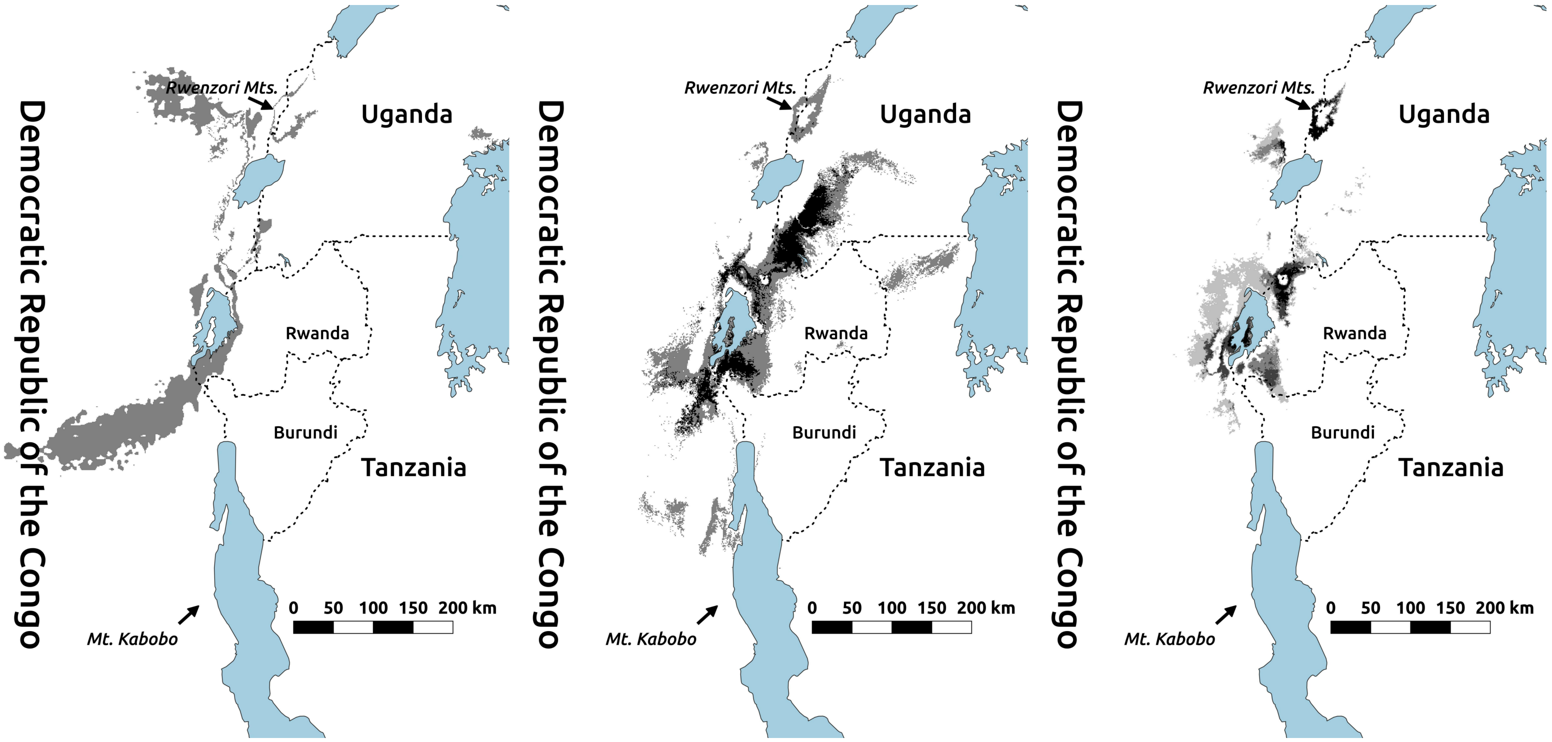

Figure C.49: *Batis diops*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

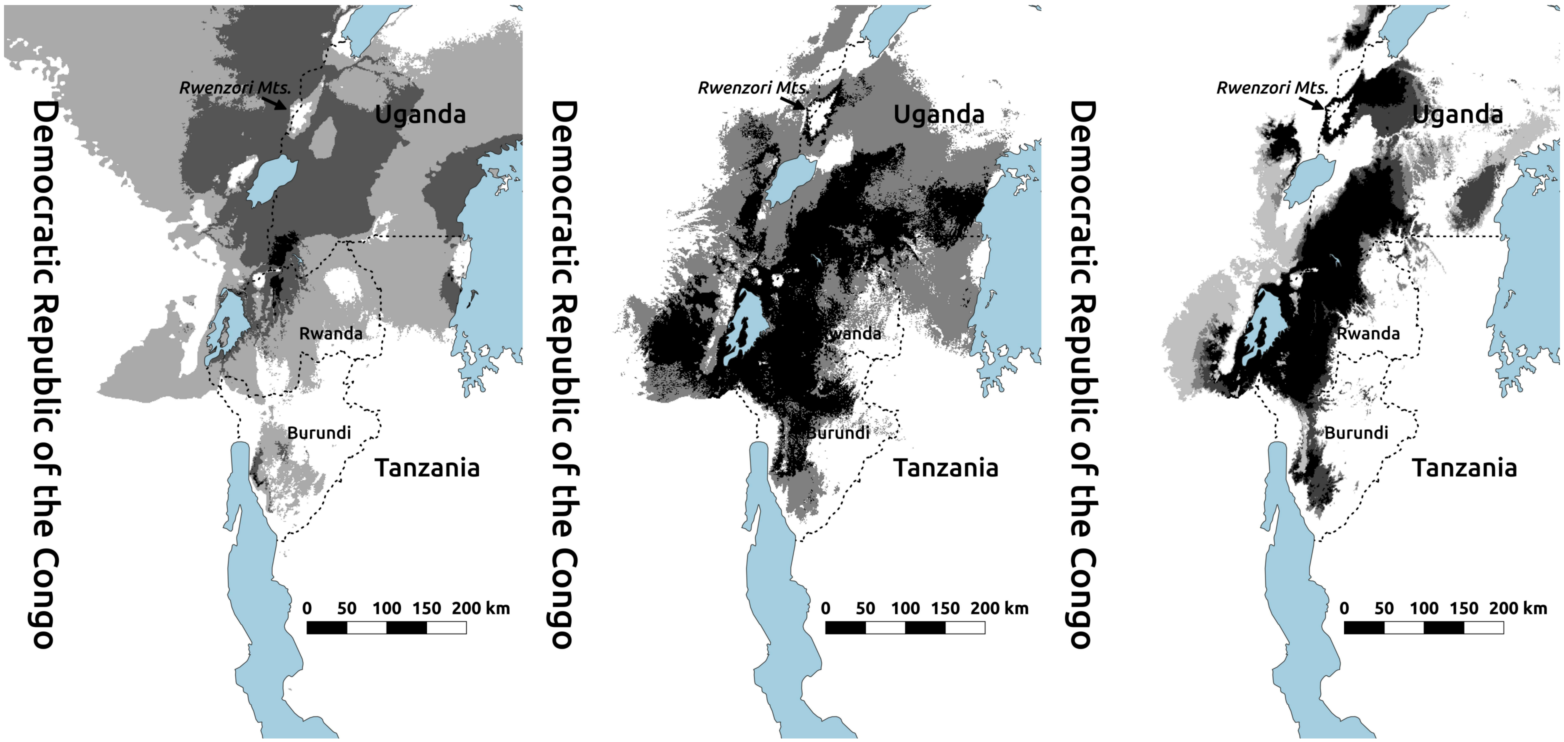

Figure C.50: *Sylvietta leucophrys.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

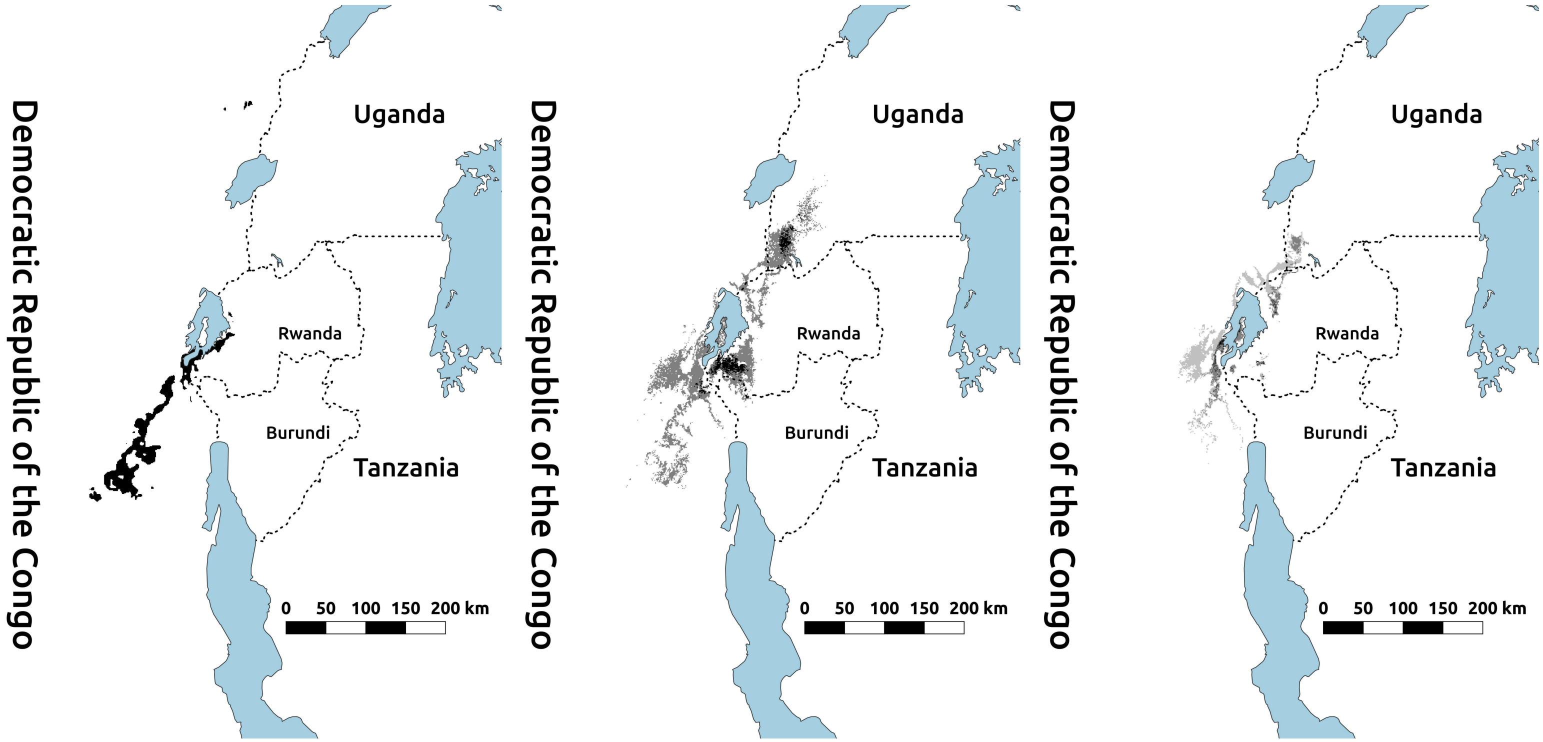

Figure C.51: *Graueria vittata*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

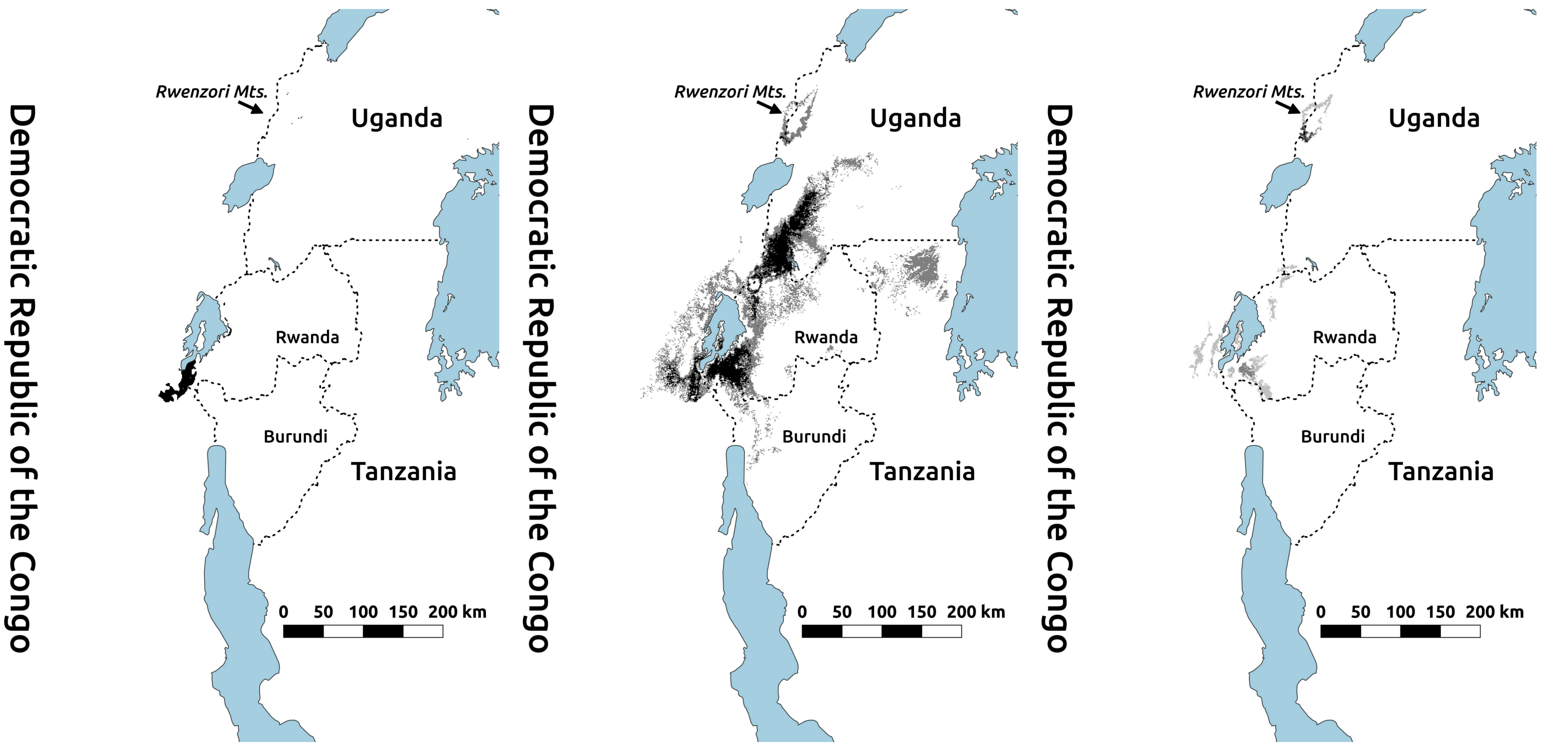

Figure C.52: *Oreolais ruwenzorii.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

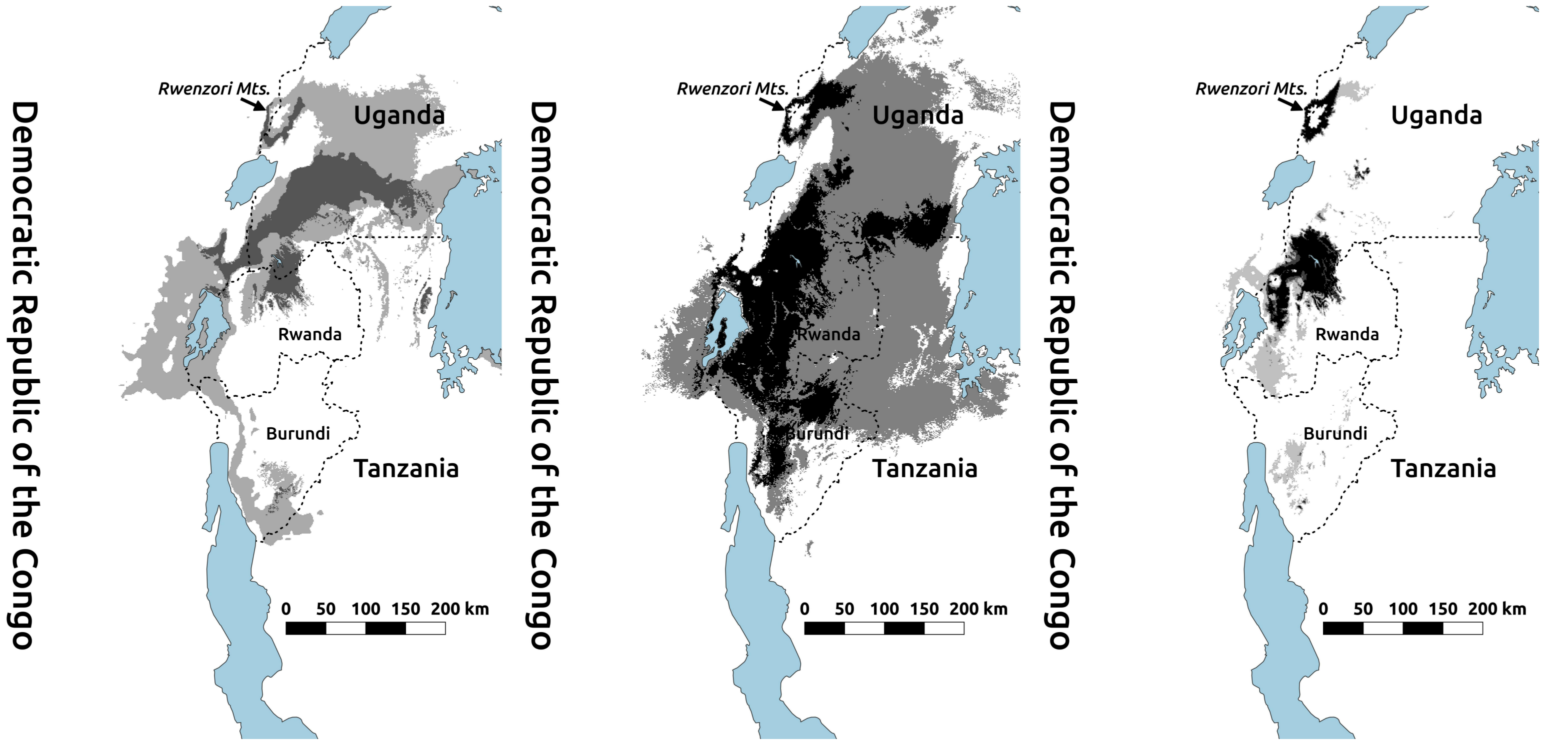

Figure C.53: *Iduna similis.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

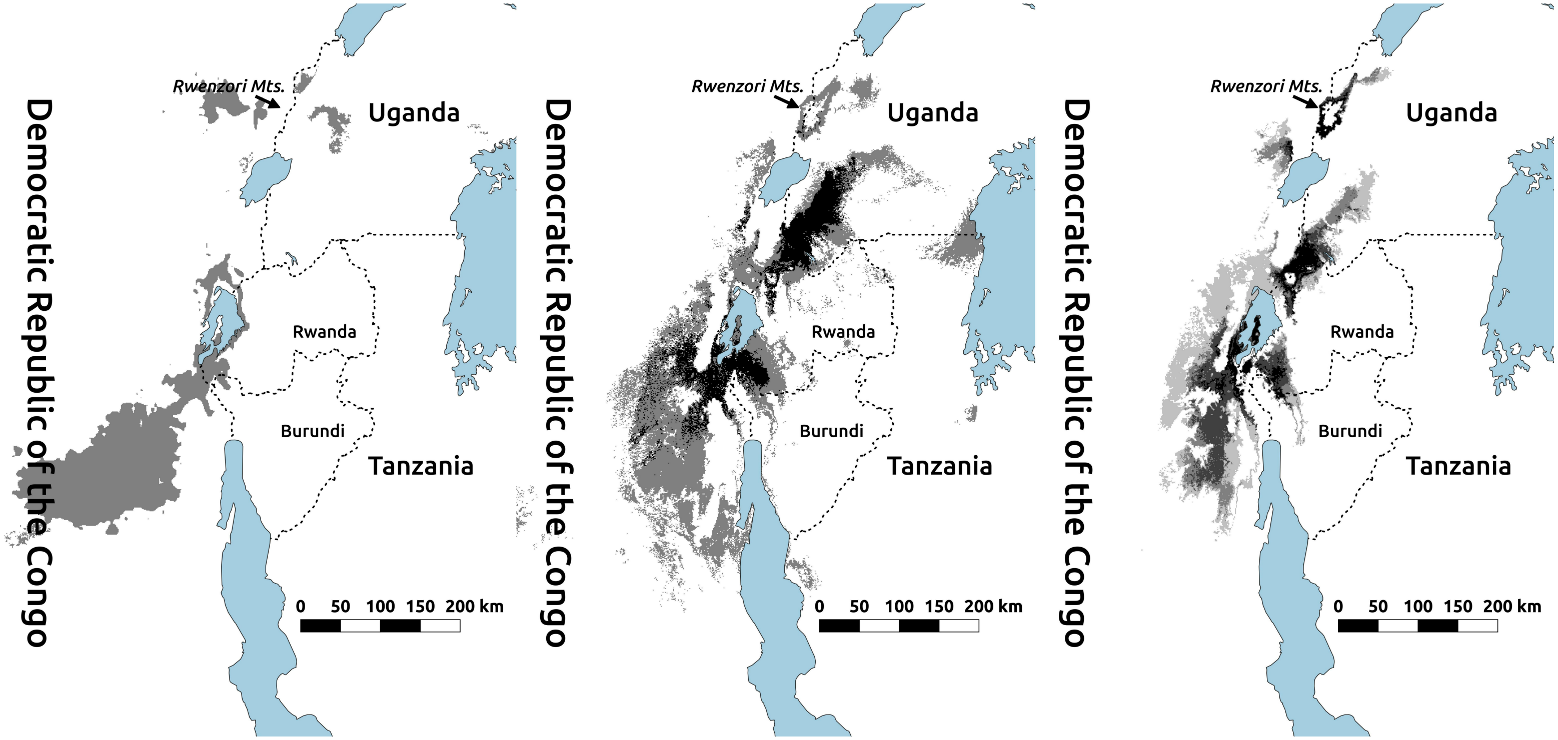

Figure C.54: *Phylloscopus laetus*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

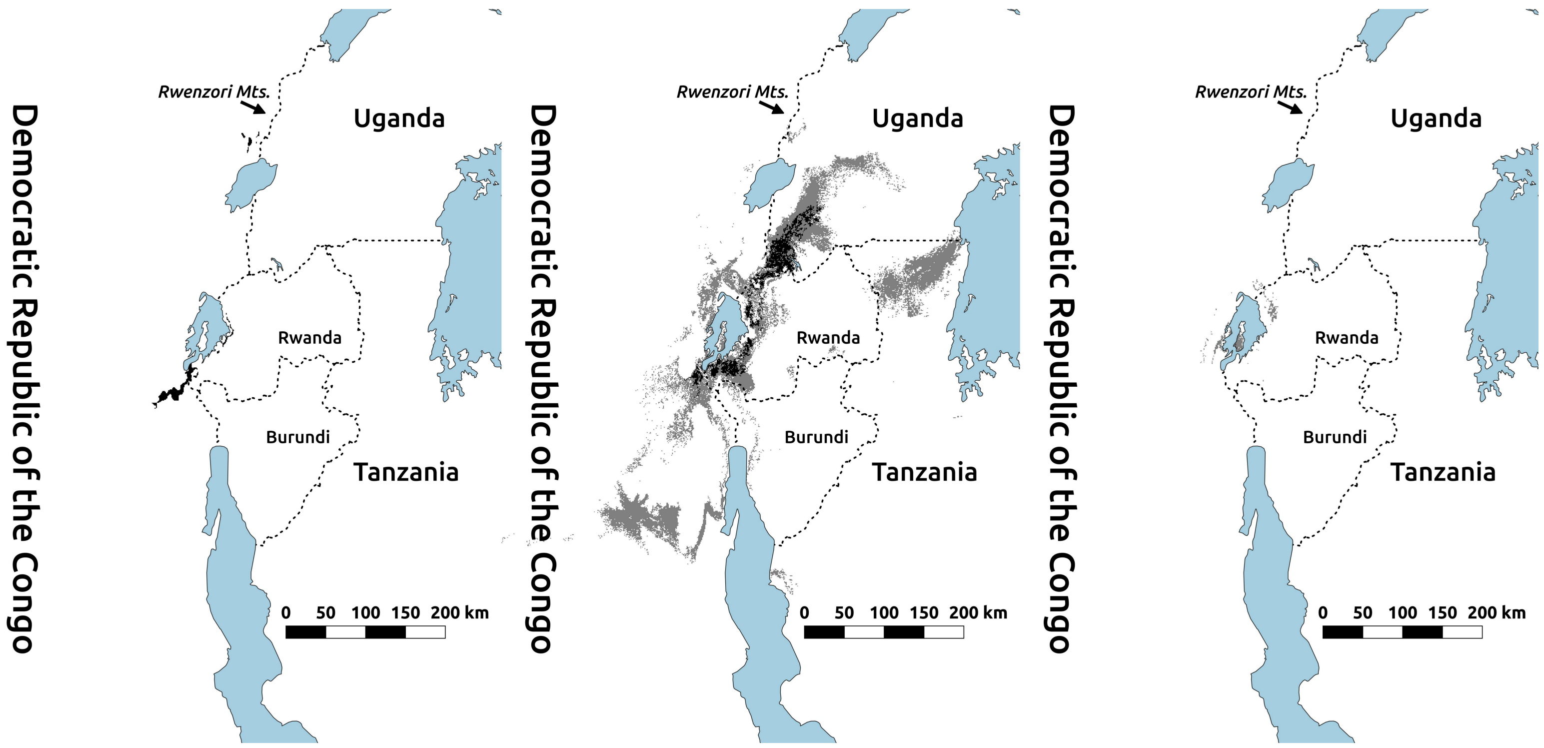

Figure C.55: *Sylvia atriceps*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

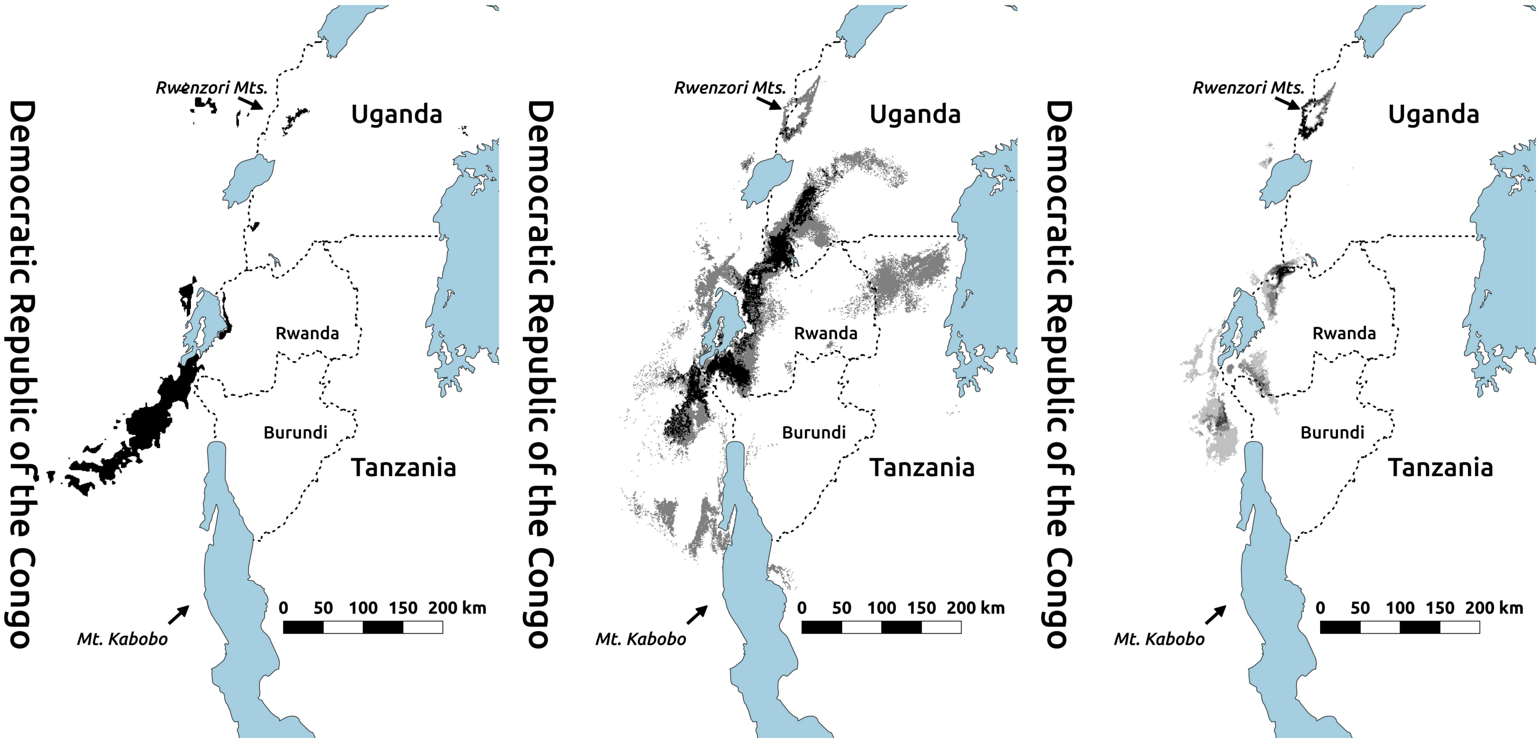

Figure C.56: *Cossypha archeri.* Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

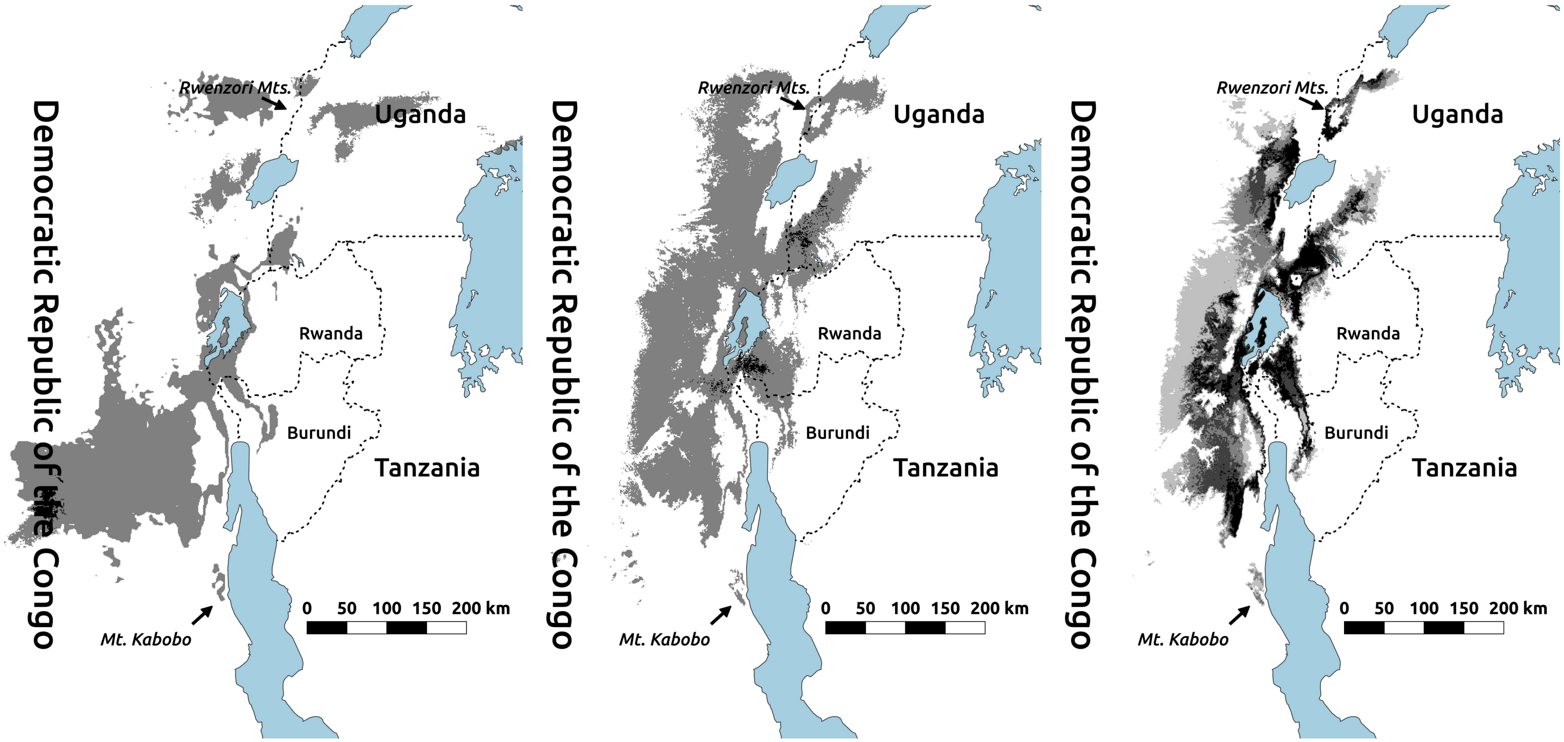

Figure C.57: *Chamaetylas poliophrys*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

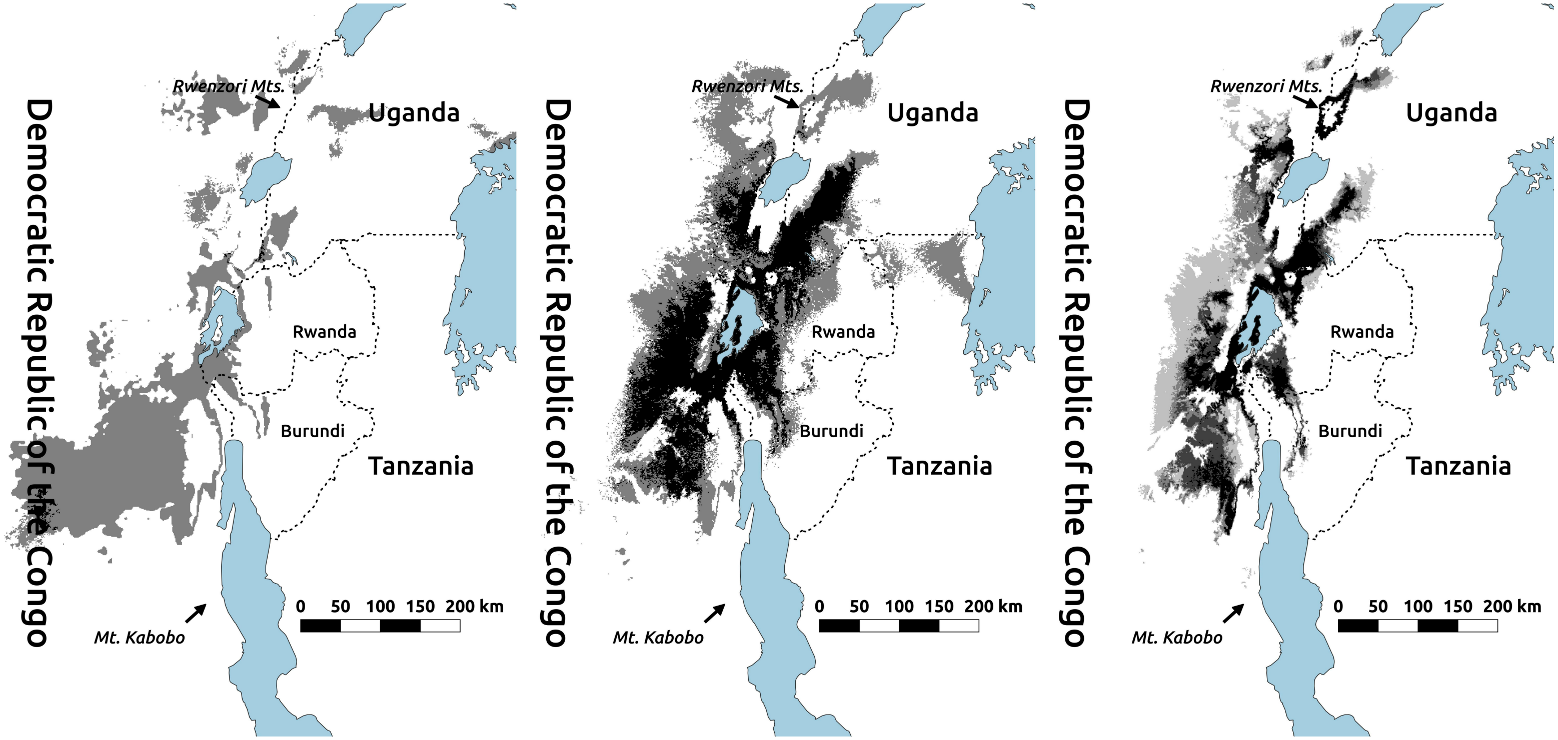

Figure C.58: *Cyanomitra alinae*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

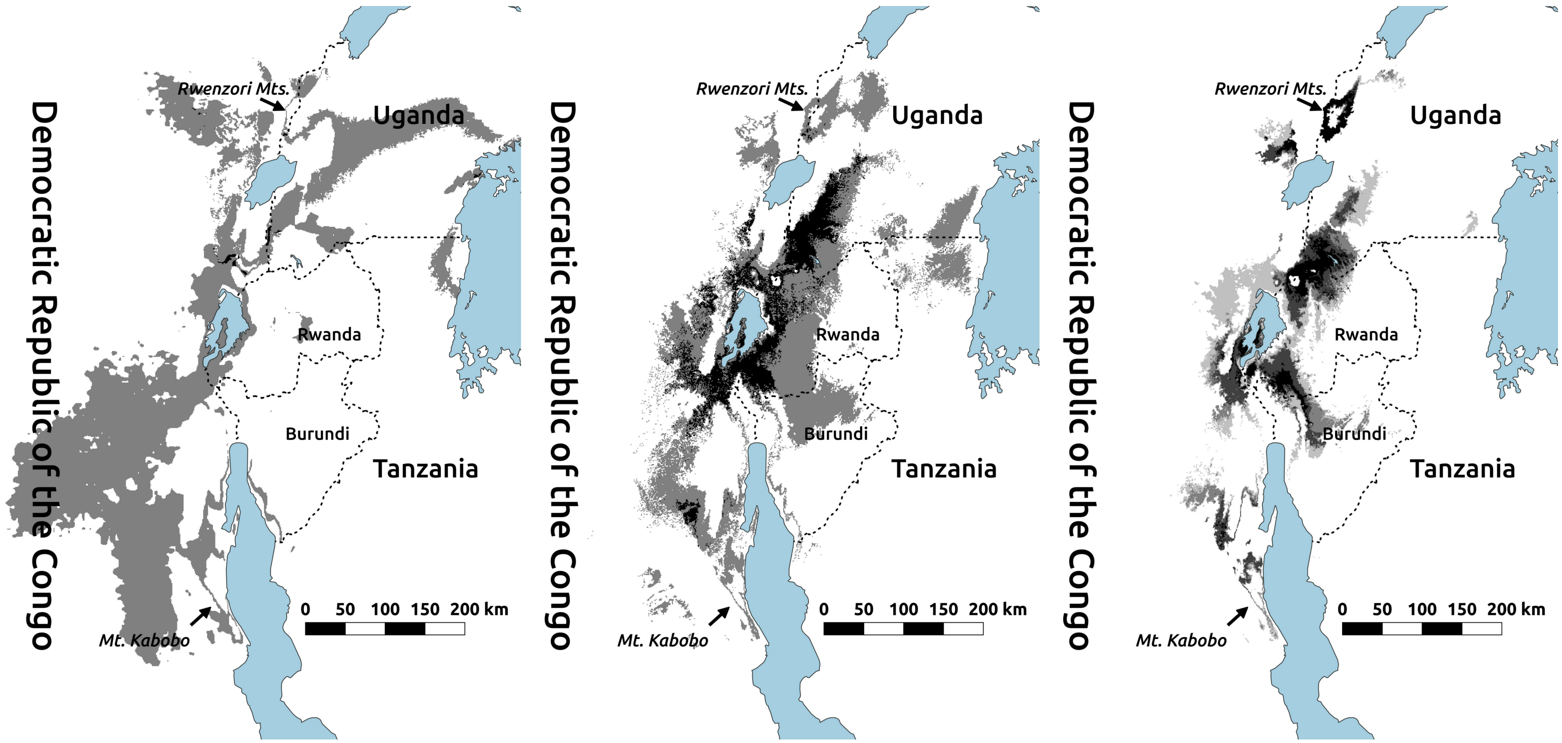

Figure C.59: *Cinnyris regius*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

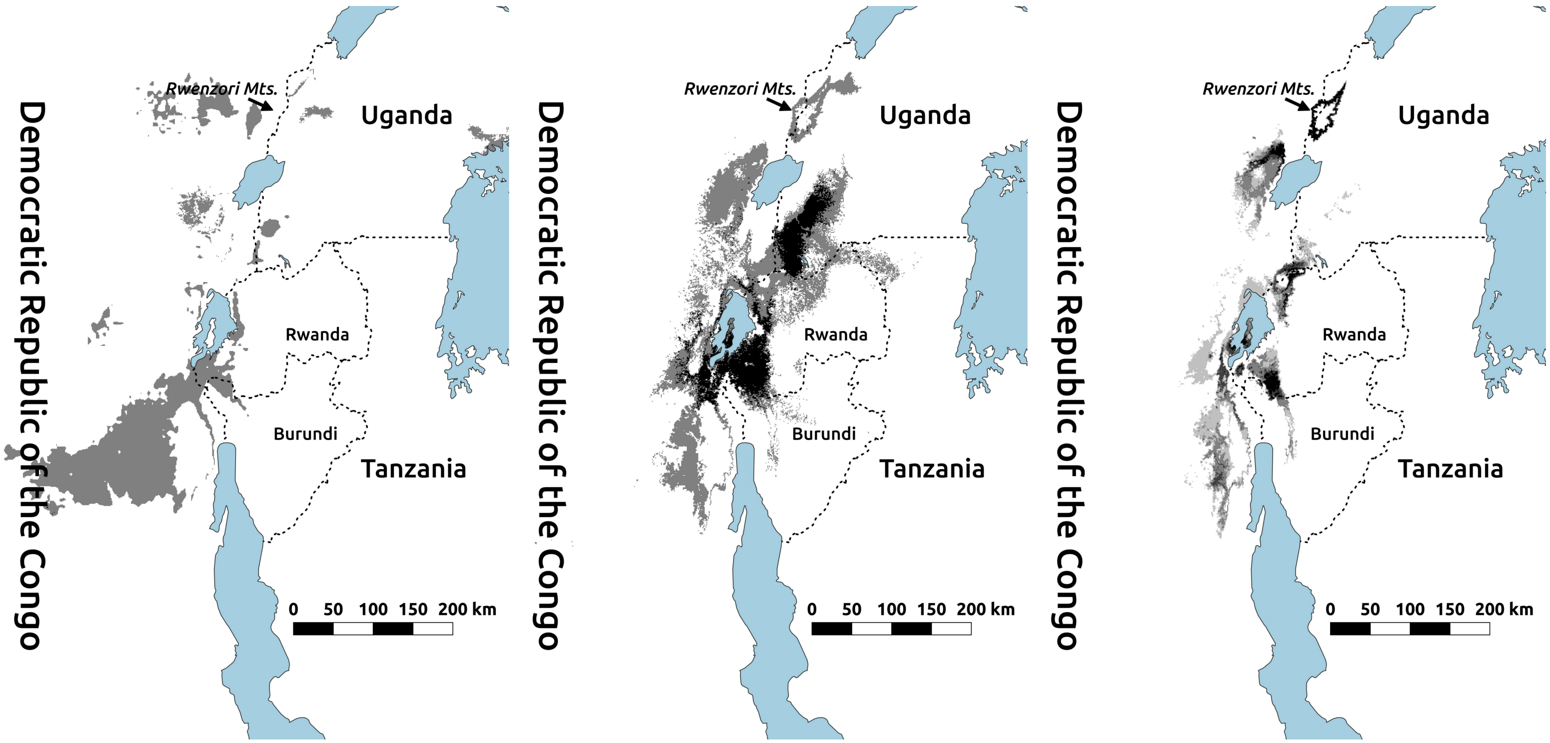

Figure C.60: *Ploceus alienus*. Maps are presented (from left to right) as concatenated past climate models (Holocene, Last Glacial Maximum, and Last Interglacial), present climate and landcover models, and future climate models (concatenation of all projections for 2070), with values assigned to concordance between models for that time period (*i.e.*, black = highest support for occurrence, white = no support for occurrence).

APPENDIX D

NICHE THEORY AND ITS RELATION TO MORPHOLOGY AND PHENOTYPE IN GEOGRAPHIC SPACE: A CASE STUDY IN WOODPECKERS (PICIDAE)

This chapter was originally published as a manuscript in the *Journal of Avian Biology* [69]. Appendices referenced in this chapter are available directly from the journal as Appendices 1-2 within Appendix JAV-01771 at `https://www.avianbiology.org/appendix/jav-01771`.

Full codes and data are available from cited information and directly from the Dryad depository [68].

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