



Modelling potential Pleistocene habitat corridors between Afromontane forest regions

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Abstract

The unusually high floral and faunal similarity between the different regions of the Afromontane archipelago has been noted by biogeographers since the late 1800s. A possible explanation for this similarity is the spread of montane habitat into the intervening lowlands during the glacial periods of the Pleistocene, allowing biotic exchange between mountain ranges. In this study, we sought to infer the existence and most likely positions of these potential habitat corridors. We focused on sixteen Afromontane endemic tree, shrub, and bird species in the Cameroon Volcanic Line, East African Rift and Great Escarpment. Species were chosen based on distribution above 1200–1500 m in at least two of the major Afromontane regions. Ecological niche models were developed for each species in the present and projected to the mid-Holocene and the last glacial maximum (LGM). Models were thresholded to create binary maps of presence/absence and then summed across taxa to estimate potential LGM and mid-Holocene distributions. We found widespread climatic suitability for our montane taxa throughout the lowlands of Central Africa during the LGM, connecting all regions of the Afromontane archipelago except the Ethiopian Highlands and the Dahomey Gap. During the mid-Holocene, we noted more limited climatic suitability for fewer species in lowland areas. Although we set out to test predictions derived from alternatively hypothesized corridors, we instead found widespread climatic suitability connecting Afromontane regions across the entire Congo Basin for all species.

Keywords Cameroon volcanic line · East African rift · Ecological niche modelling · Great escarpment · Last glacial maximum · Mid-holocene

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Introduction

Afromontane forest is characterized by a cooler, more humid climate than the surrounding lowlands. Typically found above 1200–1500 m in elevation, this ecoregion is highly segmented and is often referred to as the “Afromontane archipelago,” representing montane areas as islands separated by hotter, more arid lowlands (Moreau 1963, 1966; White 1978, 1981; Kingdon 1989). The major geographic areas of the archipelago are the East African Rift (including the Ethiopian Highlands, Albertine Rift and Eastern Arc Range) in East Africa, the Cameroon Volcanic Line in West/Central Africa, and the Great Escarpment in South Africa, with small, isolated patches also occurring in the highlands of Guinea, Sierra Leone and Liberia. These areas tend to have high species diversity (White 1981; Busmann 2004; Mutke and Barthlott 2005) and are all considered to be biodiversity hotspots of high conservation priority (White 1981; Myers et al. 2000; Schmitt et al. 2010; Mittermeier et al. 2011).

Since the late 1800s, biogeographers have noted striking floral and faunal similarity among the three disparate Afromontane forest regions, suggesting that they were connected in the recent geological past (Sharpe 1893; Moreau 1966; Hall 1973; White 1981; Prigogine 1987; Reichenow 1900). Pollen core data suggest that montane vegetation extended much further into the lowlands during the glacial periods of the Pleistocene than at present (Van Zinderen Bakker and Clark 1962; Caratini and Giresse 1979; Maley 1987, 1989), and it is possible that montane forests expanded to form habitat corridors, or biogeographical conduits for biotic exchange, that allowed species to expand their ranges among montane regions during the colder and drier periods of the Pleistocene. These ranges would have contracted subsequently, becoming interrupted and eventually separated by lowland evergreen forest during interglacial periods and the Holocene (Darlington 1957; Carlquist 1966; Moreau 1966; Hall 1973; Livingstone 1975; Maley 1991; Tosi 2008; Kadu et al. 2011). It has been estimated that a decrease in temperature of 5 °C during a glacial maximum would lower montane forest limits from ~1500 m to 500–700 m in elevation, allowing extensive spread of montane forests in lowland areas (Moreau 1963). This effect is illustrated in the present day by near-sea-level distributions of montane plants and animals on the coastal slopes of Mount Cameroon, where climate patterns enable these species to persist at low elevations (Serle 1964).

However, the location and extent of these corridors has been debated widely for lack of pollen core data from Central Africa (Hedberg 1969; Coetzee and Van Zinderen Bakker 1970; Wickens 1976). Three possible corridors have been proposed: one across the northern rim of the Congo Basin (Moreau 1963, 1966), and one through patchy montane areas in the southern Democratic Republic of the Congo, Zambia, northern Angola, and Gabon (White 1981, 1983, 1993; Fig. 1), both of which connect the Cameroon Volcanic Line to the East African Rift; and an additional corridor connecting the East African Rift and the Great Escarpment in southern Africa (Linder 1983; Fig. 1). The goal of this study was to distinguish among these classic hypotheses of Pleistocene range expansion by examining the extent and location of climatic suitability for montane species through time using paleo-projections of ecological niche models for montane species during the last glacial maximum (LGM), ~22,000 years ago, and the mid-Holocene, ~6000 years ago.

We focused on montane tree, shrub, and bird species, as they have relatively high dispersal capabilities. We analysed single species or species complexes with ranges that span multiple Afromontane regions (Moreau 1966; White 1981) and use these taxa as proxies for understanding the potential distribution of Afromontane forests as a whole (Tosi 2008;

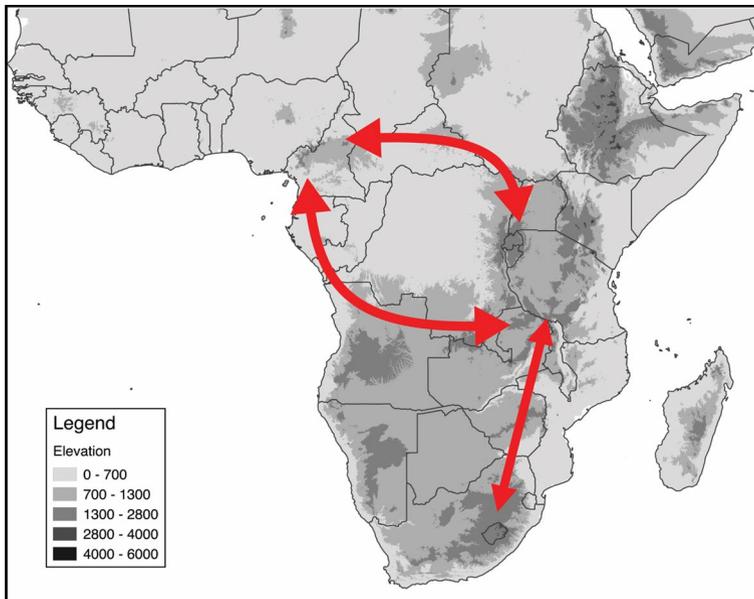


Fig. 1 Three hypothesized habitat corridors between western, eastern, and southern Afromontane regions

Kadu et al. 2011). These proxies reflect the important roles that tree, shrub, and bird species play in their ecosystems, including providing habitat (Tesfaye et al. 2013; Cooper et al. 2017), food (Kaplin et al. 1998; Menke et al. 2012), and pollination services (Johnson and Brown 2004; Farwig et al. 2006; Janeček et al. 2007; Newmark et al. 2020). We found widespread climatic suitability connecting the different Afromontane regions across Central and East Africa for all taxa in our dataset during the LGM, but more limited suitability for many taxa during the mid-Holocene. This result suggests a climatic basis for the hypothesis that species were able to expand their geographic ranges among Afromontane regions during the glacial cycles of the Pleistocene.

Materials and methods

Species selection

Bird, tree, and shrub species were used only if they were highland endemics (i.e., found exclusively above elevations of 1200–1500 m) distributed in two or more of the major Afromontane regions (Fig. 2). Special focus was given to species found on both the eastern and western sides of the Congo Basin, but species that were found in highland regions south of the Congo Basin (i.e., *Cinnyris ludovicensis*), and in South and East Africa (i.e., *Rapanea melanophloeos*) were also included. Bird species were identified using distributional information in published summaries (del Hoyo et al. 2004, 2005, 2006, 2007, 2008, 2009, 2010); tree and shrub species were identified from White (1981) and through online searches.

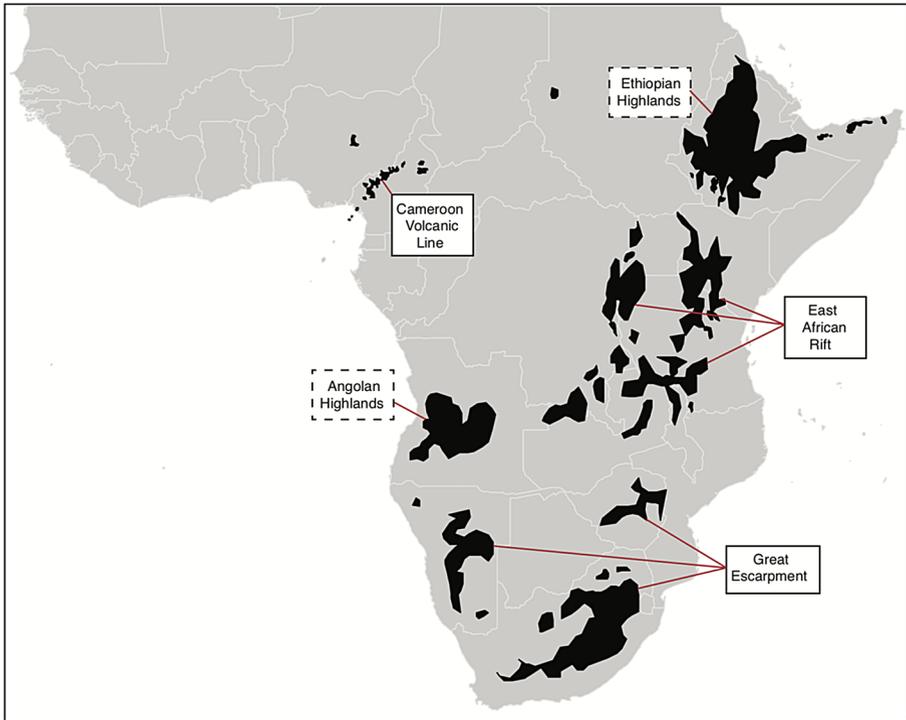


Fig. 2 The Afromontane archipelago. The Cameroon Volcanic Line, East African Rift, and Great Escarpment were the focus of this study, but the Angolan Highlands and the Ethiopian Highlands (dashed lines) were included in the distributional areas of several of our focal species

Distributional data were downloaded from GBIF. Species with the highest representative sampling were used in this study, giving a total of 10 bird species (*Apalis cinerea*, *Ceblepyris caesius*, *Cinnyris ludovicensis*, *Cisticola chubbi*, *Kakamega poliothorax*, *Onychognathus walleri*, *Oreolais pulcher*, *Ploceus baglafecht*, *Ploceus insignis*, *Sylvia abyssinica*) and 6 tree and shrub species (*Agarista salicifolia*, *Hypericum revolutum*, *Ilex mitis*, *Podocarpus latifolius*, *Rapanea melanophloeos*, *Ternstroemia polypetala*). Data were then mapped in QGIS v3.4 to check for accuracy and cleaned, removing records with no locality info or locality info far outside of the species known range, records that included only a country code or province name, or records with uncertain IDs. Records with accurate, but text-only locality information were georeferenced using Google Earth (earth.google.com) and Falling Rain Global Gazetteer Version 2.3 (www.fallingrain.com).

Ecological niche modelling

Environmental data were obtained from the WorldClim database v. 1.4 (Hijmans et al. 2005). Only mainland Africa was included in the analyses. Fifteen of the 19 bioclim variables were used in analysis at a 2.5' (~4.5 km) spatial resolution. The remaining four variables (bio8, bio9, bio18, and bio19) were excluded because they are known to hold artifacts in the form of discontinuities in the midst of continuous environmental gradients. The 15 variables were used for the LGM and the mid-Holocene under three general circulation

models (GCMs): CCSM4, MIROC-ESM, and MPI-ESM-P. To reduce collinearity effects on the resulting models, a principal component analysis (PCA) was performed on present-day bioclimatic variables and transferred to the past versions of the same set of variables.

Model calibration areas were defined as a 1000 km buffer around the known occurrence points for each species. Model calibration, creation, projection, and evaluation were carried out using the R package ‘kuenm’ (Cobos et al. 2019). To calibrate models, we created 765 candidate models for each species. Candidate models included all combinations of three sets of environmental predictors (PCAs 1–6, 1–5, 1–4), 17 regularization multiplier values (0.1–1.0 at intervals of 0.1, 2–6 at intervals of 1, and 8 and 10), and all combinations of four feature classes (linear=l, quadratic=q, product=p, and hinge=h; Cobos et al. 2019). Models were run using maximum entropy machine-learning algorithms in MAXENT v. 3.4 (Phillips et al. 2006); best models were chosen based on significant partial ROC scores (Peterson et al. 2008; 500 bootstrap replicates, $E=5\%$), omission rates $<5\%$ based on a modified least training presence thresholding (Anderson et al. 2003; $E=5\%$), and AICc scores of ≤ 2 to minimize model complexity (Warren and Seifert 2011). This model selection procedure identified the optimal parameter set to be used for final model creation.

Final models were created for each species using the full set of occurrence records and the parameters chosen during model calibration (see above), also using the ‘kuenm’ package. Models were run in MAXENT with 10 bootstrap replicates and logistic output formats. After models were run in the present, they were checked for consistency with the species known distribution and transferred to the LGM and mid-Holocene for each of the three GCMs. The mobility-oriented parity (MOP) index was used to test for model extrapolation (Owens et al. 2013). Models were visualized in QGIS 3.4 and thresholded using a modified least training presence thresholding ($E=5\%$) to create binary maps of presence/absence. Models from each time period were summed to estimate potential LGM and mid-Holocene distributions (Devitt et al. 2013; Yannic et al. 2014).

Results

For all species analysed, our models suggested suitable climate, defined as climate for which a species was projected to be able to be present after binary thresholding, connecting Afromontane regions on either side of the Congo Basin during the LGM. Indeed 20–40% of the species showed connections across the Congo Basin during the mid-Holocene (Figs. 3, 4). Broadly, trees/shrubs and birds showed different distributional histories but overall similar patterns. The southern route between the Cameroon Volcanic Line and the East African Rift appears to have been climatically suitable for a higher proportion of bird species than plant species during the mid-Holocene, but both routes were climatically suitable for nearly all species during the LGM. In tree and shrub species, both the northern and the southern routes were climatically suitable for all species during the mid-Holocene. We noted widespread climatic suitability across lowland regions of Central and West Africa during the LGM. Large areas of unsuitable climate separated the East African Rift and the Great Escarpment for all species during the mid-Holocene; however, during the LGM, continuous suitable habitat was inferred between these two regions for 30–40% of the bird species in this study and all tree/shrub species.

Although we did not focus on species occurring in the Angolan and Ethiopian Highlands, they were included in the actual and potential distributions of many species. Our models suggested that climatically suitable habitat connected the Angolan

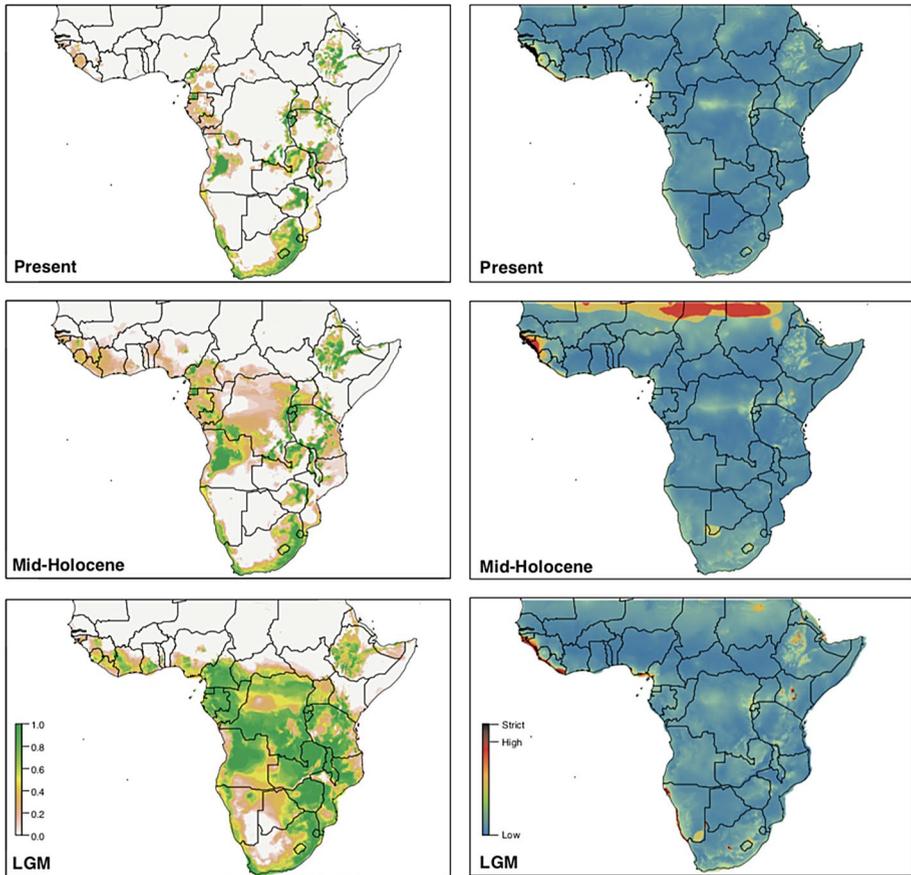


Fig. 3 Left: Present-day and paleo-projections of ecological niche models for a variety of Afromontane tree and shrub species during the present, the mid-Holocene, and the last glacial maximum. The scale bar represents the proportion of study species found in that area for each time period. Right: An averaged MOP analysis for extrapolation for each of the three time periods. The scale bar represents the extrapolation risk from strict to low extrapolation

Highlands to the rest of the Afromontane system during LGM, but such was not the case for the Ethiopian Highlands, which were separated by climatically unsuitable habitat for all species during all three time periods included in this study. Similarly, the Dahomey Gap in Benin and Togo in West Africa remained unsuitable from LGM to present for all species.

The averaged MOP index identified several areas of heightened or strict extrapolation across taxa, none of which significantly impacted our study system (Figs. 3, 4). Areas of extrapolation included the Sahara, Kalahari and Namib deserts and the westernmost tip of West Africa. These areas should be interpreted with caution due to increased model uncertainty (Owens et al. 2013), but do not affect the results presented above.

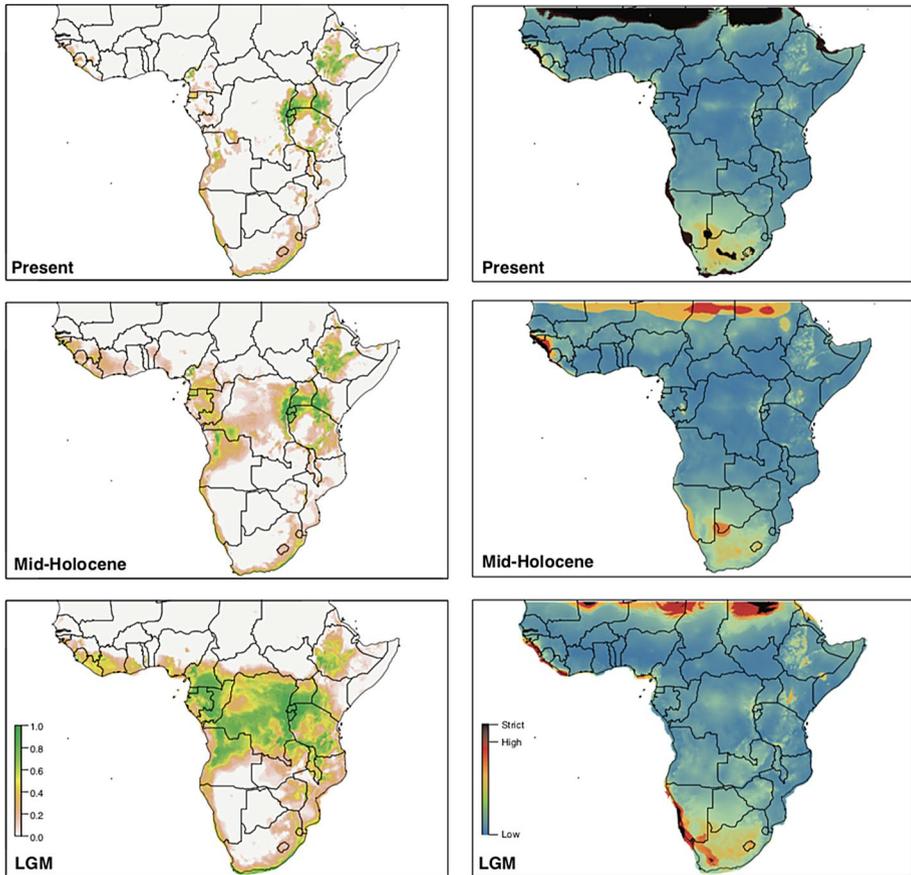


Fig. 4 Present-day and paleo-projections of ecological niche models for a variety of Afromontane avifauna during the present, the mid-Holocene, and the last glacial maximum. The scale bar represents the proportion of study species found in that area for each time period. Right: An averaged MOP analysis for extrapolation for each of the three time periods. The scale bar represents the extrapolation risk from strict to low extrapolation

Discussion

The extensive literature regarding terrestrial montane biogeography of the African continent historically has identified three potential routes for biotic exchange among Afromontane forest regions during the Pleistocene glaciations and the Holocene (Moreau 1966; Hall 1973; White 1981). All three have been invoked to explain the unusual floral and faunal similarity among the Cameroon Volcanic Line, East African Rift and, Great Escarpment (Moreau 1963, 1966; White 1981, 1983, 1993; Linder 1983; Fig. 1). However, the location, extent, and even existence of these corridors have been debated (Hedberg 1969; Coetzee and Van Zinderen Bakker 1970; Wickens 1976), particularly given the difficulty of obtaining pollen core data from Central Africa. Here, we investigated the climatic feasibility of these habitat corridors using species ecological niche modelling for a variety of

Afromontane tree, shrub, and bird species during the last glacial maximum (~22,000 yrs. ago), the mid-Holocene (~6,000 yrs. ago), and the present.

It is likely that several of the species in this study represent cryptic species complexes. For example, the West African population of *Cisticola chubbi* is considered by some authors to be a separate species, *C. discolor* (e.g., Maisels and Forbeseh 1999; Languy and Motombe 2003), but is considered conspecific by others based on vocal data (Urban et al. 1997). Few dated phylogeographic studies have been done on many of these taxa, but all have exhibited patterns of diversification during the Pleistocene (Kadu et al. 2011; Meseguer et al. 2013; Migliore et al. 2020; Cooper et al. 2021). Earlier divergence dates would not be unexpected (e.g., Ting 2008; Taylor et al. 2014; Pokorný et al. 2015; Mikula et al. 2021) but also would not preclude the possibility of gene flow between these montane areas during the glaciation cycles (Nosil 2008; Feder et al. 2012; Martin et al. 2013). If these taxa represent widespread species, as opposed to species complexes, they may be more generalist than the small range endemics found in the same mountain ranges (Hanski and Gyllenberg 1997; Wilson et al. 2004; Jetz et al. 2007; Büchi and Vuilleumier 2014), or at least have much greater dispersal abilities (Lester et al. 2007; Büchi and Vuilleumier 2014). These abilities may have allowed them to take advantage of a wider range of potentially suitable habitats connecting different Afromontane regions, especially if these species are able to inhabit both high elevation rainforest and grassland (Wilson et al. 2004; Jetz et al. 2007).

Although we set out to discriminate among alternate positions of hypothesized corridors of suitable climate north and south of the Congo Basin during the LGM, we found widespread climatic suitability connecting Afromontane regions across the entire Congo Basin for all taxa included in this study (Figs. 3 & 4). Evidence pointing to the existence of climatically suitable corridors, particularly the southern corridor, was available for some species during the mid-Holocene (Figs. 3 & 4), when the global climate was approximately midway between the present and the LGM, suggesting that climate was suitable for some species to expand their geographic ranges through biotic exchange among Afromontane regions as recently as 6000 years ago. A similar pattern was also seen in the corridor proposed to link the Eastern Arc Range and the Great Escarpment (Fig. 3), where climatic connectivity between these ranges existed for some species during the mid-Holocene, and widespread connectivity was available for all species during the LGM (Figs. 3 & 4).

The possibility of widespread habitat suitability for high elevation forest types in lowland Central Africa during the Pleistocene aligns with what little is known about this region from pollen records. Pollen from the genus *Podocarpus*, normally associated with montane cloud forest, has been detected in palynological records from the Congo River fan as early as 1.05 million years ago (Dupont et al. 2001). Records of *Podocarpus* and another montane species used in this study, *Ilex mitis*, have been found in pollen cores at 700 m in the Batéké plateau in the Republic of the Congo that date back to the LGM (Elenga et al. 1994). *Podocarpus* pollen continued to be found in lowland Congo Basin palynological records until the beginning of the late-Holocene and occurred simultaneously with pollen from wet evergreen taxa (Maley 1997). These palynological findings, as well as modelled broad-scale vegetation changes across Africa, appear to be closely linked to glacial cycles (Maley 1997; Dupont et al. 2001; deMenocal 2004; Anhuf et al. 2000, 2006) and, as a result, the extension of *Podocarpus* into lower elevations likely occurred synchronously between Central and East Africa (Maley 1997). Although only one high elevation genus is strongly represented in pollen core records, this genus is indicative of shifts in entire Afromontane forest communities (Maley 1997; Dupont et al. 2001). As a dioecious species, *Podocarpus* is prone to overrepresentation in the palynological records compared

to many other high elevation tree and shrub species which, depending on their pollination syndromes, may be palynologically silent (Bush and Rivera 2001; Dupont et al. 2001; Johnson and Brown 2004; Farwig et al. 2006; Janeček et al. 2007; Nsor et al. 2019; Newmark et al. 2020).

More broadly across Africa, some areas that present climatic barriers to biotic exchange today continued to present barriers throughout the mid-Holocene and the LGM, including the Dahomey Gap, a relatively dry, savannah region separating the upper and lower Guinean rainforests of West Africa (Figs. 3 & 4). Pollen cores indicate that this savannah has remained stable since at least the mid-Holocene (Marchant and Hooghiemstra 2004; Salzmann and Hoelzmann 2005), but phylogeographic analyses with species divergence dates estimate that this savannah likely has been present since the Miocene (e.g., Fuchs and Bowie 2015; Demenou et al. 2018). The Ethiopian Highlands also remained separated, in this case by a climatic barrier, from the rest of the Afromontane archipelago (Figs. 3 & 4), possibly explaining the biological distinctness of this region (Prigogine 1987; Poynton 1999; Williams et al. 2004), and the relatively deep genetic divergences inferred among its endemic species and their close relatives in other Afromontane areas (Reyes-Velasco et al. 2018; Zinner et al. 2018; Šmíd et al. 2019).

Although correlative ecological niche models effectively characterize the geographic positions and extent of areas of climatic suitability, they do not allow us to determine direction of dispersal, historical timeline of colonization, nor polarity of range expansion. However, several dated phylogeographic studies of Afromontane species have not only suggested similar areas of habitat suitability, but also included directionality. For instance, phylogeographic studies of the Afromontane tree species, *Prunus africana* and *Podocarpus latifolius*, suggested colonization of western Central Africa from East Africa through a northern dispersal route for *P. africana*, and through northern and southern dispersal routes for *P. latifolius* with divergence dates around the LGM for both species (Kadu et al. 2011; Migliore et al. 2020). A study of distributional patterns of the Afromontane avifauna also suggested a general east-to-west pattern of range expansion (Prigogine 1987). Phylogenetic data appear to support this pattern, with Cameroonian Afromontane bird populations from a variety of species embedded within Angolan-East African clades (Vaz da Silva 2015), and a Pleistocene divergence between East African and Angolan Turaco species (Njabo & Sorenson 2009). A phylogeographic study of *Chlorocebus* monkeys suggested faunal exchange via the northern route during the LGM but, in this case, dispersal from the west, resulting in colonization of the east (Tosi 2008). Dispersal from the East African Rift southward to the Great Escarpment was supported by a phylogeographic study on *Lygodactylus* geckos (Travers et al. 2014), from the Eastern Arc Mountains southwards to the Rift Mountains in *Arthroleptis* frogs (Blackburn and Measey 2009) and from the Great Escarpment northward to the East African Rift for *Euryops* plants (Devos et al. 2010), likely in all cases during globally cool-climate periods. These previous studies thus support the existence of Pleistocene habitat corridors among Afromontane regions and suggest multi-directional exchanges among regions.

Studies of the effects of Pleistocene glaciations on tropical montane taxa are only now accumulating, resulting in remarkable insights into some of Africa's most understudied, highly endemic, terrestrial flora and fauna—much of which has been formally classified as high-value conservation urgency (Myers et al. 2000; Blackburn and Measey 2009; Schmitt et al. 2010; Kadu et al. 2011; Mittermeier et al. 2011; Vaz da Silva 2015; IUCN 2020). Although the overwhelming majority of research in the tropics has focused on diversification in hypothesized lowland rainforest refugia (Fjeldså and Bowie 2008; Gomez et al. 2009; Dainou et al. 2010; Dauby et al. 2010; Lowe et al. 2010; Born

et al. 2011; Budde et al. 2013; Hardy et al. 2013; Ley et al. 2014; Duminil et al. 2015; Faye et al. 2016; Ley et al. 2016; Silva et al. 2019), this study suggests that the Pleistocene climatic oscillations also served as an historical opportunity for faunal admixture, and possibly even a homogenizing period among disparate montane areas, at least for species included here. These results accord well with predictions developed by Peterson and Ammann (2013), in which certain world regions (e.g., tropical montane regions) exhibited phases of isolation and speciation during the glacial periods (e.g., the Amazon Basin) and other regions were characterized by isolation/speciation phases during the *inter*-glacial periods.

Although the extent of potential habitat change in the Central African lowlands suggested by our models is high, our general results are in line with previous studies based on pollen core data which have concluded a spread of montane forest into the lowlands during the LGM, with the caveat that sampling is limited (Van Zinderen Bakker and Clark 1962; Caratini and Giresse 1979; Maley 1987, 1989, 1997; Dupont et al. 2001; reviewed in Couvreur et al. 2020), and with recent global paleoclimate models that suggest a transition from tropical rainforest to warm temperate woodland and temperate broadleaf evergreen forest in Central Africa during the LGM (Allen et al. 2020). These recent models are a distinct shift away from previous hypotheses of a transition from lowland rainforest to strict savannah in Central Africa during the Pleistocene (Coetzee 1964; van Zinderen Bakker and Coetzee 1972; Anhuf 2000, 2006), with some authors now suggesting that a widespread aridification and expansion of grasses during the glaciation cycles may have been generally restricted to eastern Africa (Ravelo et al. 2004; reviewed in Couvreur et al. 2020). Dupont et al. (2001) notes that it is difficult to distinguish if grass (Poaceae) and sedge (Cyperaceae) pollen in his Central African palynological records originated in swampy vegetation along rivers, or in open savannah/woodland, and suggested that abundant *Podocarpus* pollen in lowland Central Africa during glacial cycles supported a cool, yet humid climate. Our results, based on three widely used general circulation models, also suggest that these climate projections support a cool, humid climate for Central Africa during the LGM.

In addition to testing classical hypotheses of Afromontane biogeography, in this study we also demonstrate ways in which paleo-distributional projections of ecological niche models can be employed for practical purposes, or strategically employed in particular geographic regions where *in situ* data collection has been historically challenging or is logistically unfeasible today. Finally, the results presented here suggest fruitful opportunities for field studies and surveys targeting the unstudied, or intervening highlands among Central Africa's reasonably well-known montane biotic regions. This study lends urgency to the task of collecting corroborating pollen-core data, as well as safe-guarding the few formally designated protected areas of the central Afromontane highlands.

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Authors' contributions KEA, RMB and ATP conceived the ideas; KEA, WPTN, BF, and JCC collected and analysed the data; and KEA led the writing, with assistance from RMB, ATP, WPTN, and JCC.

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dl.zepi4n, <http://doi.org/10.15468/dl.xw40dj>, <http://doi.org/10.15468/dl.ju9mu4>, <http://doi.org/10.15468/dl.oayvyx>, <http://doi.org/10.15468/dl.v4g9ms>

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval All procedures involving animals followed approved IACUC protocols and were conducted with the appropriate permits.

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