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Uncovering cryptic diversity and refugial persistence among small mammal lineages across the Eastern Afromontane biodiversity hotspot



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ABSTRACT

The Eastern Afromontane region of Africa is characterized by striking levels of endemism and species richness accompanied by significant conservation threat, a pattern typical across biodiversity hotspots. Using multi-locus molecular data under a coalescent species tree framework we identify major cryptic biogeographic patterns within and between two endemic montane small mammal species complexes, *Hylomyscus* mice and *Sylvivorex* shrews, co-distributed across the Albertine Rift and Kenya Highlands of the Eastern Afromontane Biodiversity Hotspot (EABH). Hypotheses put forward to account for the high diversity of the region include retention of older palaeo-endemic lineages across major regions in climatically stable refugia, as well as the accumulation of lineages associated with more recent differentiation between allopatric populations separated by unsuitable habitat during periods of Pleistocene aridification. Sympatric pairs of sister lineages were found to have significantly older divergence times than allopatric pairs. Genetic analyses and historical distribution modeling suggest that regional meta-populations have persisted since the Pliocene to mid-Pleistocene across a climatic gradient from the Albertine Rift in the west to the Kenya Highlands in the east for both focal taxa. Differing patterns of regional sub-division and demographic expansion were detected and are consistent with differing life histories as well as shared responses to regional variation in stability of suitable habitat. There is also strong support in both mice and shrew species for Late Miocene divergence with subsequent range expansion into sympatry in previously unidentified cryptic species pairs. These results highlight the broad temporal scale at which climatic and geological changes may have facilitated rare dispersal events between montane habitats as well as the long-term persistence of populations in both the Albertine Rift and the Kenyan Highlands that together contributed to the high species diversity and endemism in the EABH.

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1. Introduction

The climatic oscillations of the Quaternary period (2.6 Ma – present) have been identified as a major factor in shaping geographic ranges, biodiversity gradients, and spatial patterns of population genetic structuring in extant and extinct organisms among temperate regions (reviewed in Hewitt, 2000; Hewitt and Lister, 2004), in contrast to more recent studies of Southern Hemisphere and tropical fauna that have revealed causal processes that reach back into the Miocene (Roy et al., 2001; Fjelds and Bowie, 2008). While it is no longer the case that the biogeographic history of African tropical fauna has been neglected (Nicolas et al., 2008a,b, 2011; Bryja et al., 2010; Lorenzen et al., 2012), the East African

montane region, which stretches from the highlands of Ethiopia in the north to Mozambique in the south, remains significantly understudied, despite the fact that it contains one of the largest concentrations of threatened endemic species on earth, leading to its designation as the Eastern Afromontane Biodiversity Hotspot (Brooks et al., 2004; Kuper et al., 2004). Among groups that have been surveyed for patterns of phylogeographic structure, including birds, mammals, insects and plants (e.g. Bowie et al., 2004, 2006; Huhndorf et al., 2007; Voje et al., 2009), many are endemic to the region, and most are under threat from habitat destruction in this resource rich and increasingly densely populated part of Africa (Dudley et al., 2002; Fjelds and Burgess, 2008). The genetic diversity and structure of taxonomic groups from these montane regions has not been well studied and is particularly sparse for the Albertine Rift (hereafter AR) and Kenyan Highlands (hereafter KH) regions of the Eastern Afromontane hotspot. The AR has been identified as a biodiversity hotspot within this extensive montane

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region and which has the second highest concentration of mammalian richness on earth (Ceballos et al., 2005) and possesses strong biogeographic affinities with the KH that are as yet little understood from an evolutionary and phylogeographic perspective (Plumptre et al., 2007).

The current disjunct distributions and phylogeographic patterns of numerous African montane fauna led to proposals for various forest refugial models (i.e. Haffer, 1969) whereby forest expansions during interglacials connected vertebrate populations that had been isolated during forest contraction phases associated with the xeric conditions of glacial maxima (Diamond and Hamilton, 1980; Kingdon, 1981). Isolation of forest refuges during glacial maxima and recurrent expansions and contractions of forest habitats coincident with a cyclical “Pleistocene breathing model” (Jesus et al., 2006) has likely played a prominent role in shaping current species distributions and patterns of genetic diversity within and among wet tropical forests in Africa (Levinsky et al., 2013), but its role as a driver of tropical diversification in vertebrates is being increasingly called into question. Fjeldså and Bowie (2008) found general support for a refuge model of montane forest fragmentation that facilitated speciation of African montane birds, but the timing of these events largely predated the Pleistocene, thus ruling out a predominate role for Pleistocene forest refugia in generating present day diversity patterns. They argued instead for a model where pulsed expansion and contraction of montane forest during the Pliocene led to long-term lineage persistence and diversification in climatically stable refugial hotspots rather than increased rates of diversification *per se* in Pleistocene refugia. In contrast, several recent studies found evidence that contractions of forest cover resulting from Quaternary climatic fluctuations were congruent with observed patterns of genetic divergence in montane rodents (Huhndorf et al., 2007; Nicolas et al., 2008b) and flightless crickets (Voje et al., 2009) at both the intra- and inter-specific levels. Overall, however, there is a growing body of evidence that supports long-term persistence of species within climatically stable refugia coupled with relatively rare speciation events over a much longer time-frame than originally envisioned in the Pleistocene refugia model. Lineage diversification in African montane birds commenced as far back as the Late Miocene in birds and even the Oligocene in Afromontane reptiles (Voelker et al., 2010; Tolley et al., 2011; Fjeldså et al., 2012). Nonetheless, under either of these competing scenarios, (refugial persistence with rare speciation vs. accelerated Pleistocene diversification), without maintenance of isolation in the Pleistocene many of these patterns of endemism would have been erased.

Our comparative study uses multi-locus genetic variation within and among co-distributed populations of two endemic small mammal taxa that are restricted to montane rainforest in the AR and KH regions to test alternative hypotheses of range fragmentation and fusion in the context of Plio-Pleistocene climatic cycles and Neogene African plate uplift and East African Rift formation. Broad geographic sampling of genetic data is used to uncover historical connections within and among species as well as the timing and extent of population-level size changes which allows for inference of the spatial and temporal framework of population persistence (i.e. historically stable forest refugia). We not only use multi-locus coalescent species delimitation and species tree methods to infer the presence and distribution of allopatric divergent lineages, but also use these tools to detect cases of emergent reproductive isolation among cryptic species that have become sympatric. To test alternative hypotheses regarding how climatic and environmental changes may have shaped patterns of biodiversity, we used broad geographic sampling of two co-distributed endemic small mammal species complexes and their newly uncovered cryptic sister taxa from Eastern Afromontane forests: the *Hylomyscus denniae* group (montane wood mouse) and

Sylvisorex granti group (Grant's forest shrew). These high altitude endemics have been documented as among the most abundant species present in the high altitude zones of the AR and KH based on comprehensive small mammal surveys (Kerbis Peterhans et al., 1998; Carleton et al., 2006), yet are restricted to wet montane forest and forest mosaic habitats (Fig. 1). These shared distribution limits make these taxa well-suited for inferring how and when historical changes shaped patterns of population structure and cryptic biodiversity. In addition, their restriction to high-elevation forested habitat makes them ideal for testing inferences on the role of refugia in structuring diversification. Although these two taxa share distribution limits and ecological tolerances, differences in micro-habitat associations, dispersal abilities, body sizes, and diets may have resulted in differential responses to palaeoclimatic fluctuations.

Here we use multi-locus genetic data sets from these two co-distributed small mammal genera to test hypotheses on refugial isolation and montane diversification. Widespread sampling of two major sub-regions within the Eastern Afromontane region, the Albertine Rift (AR) and the Kenyan Highlands (KH), presents an opportunity to compare an ancient and topographically complex area where uplift was in place by the mid-Miocene (AR; Roberts et al., 2012), to a less topographically complex area of predominately volcanic highlands, whose origins span a much greater time range from the mid-Miocene to the Pleistocene (KH; Wichura et al., 2010). In so doing, this comparison can potentially uncover what effect the climatic and geomorphological changes since the Miocene have had on mammals distributed across regions separated by a 500 km montane forest gap (i.e. “Uganda gap” in Fig. 1).

We analyze demographic and temporal phylogenetic data to specifically test the following hypotheses: (1) Does isolation, divergence, and subsequent range expansion drive evolutionary diversification such that sympatric species pairs have older divergence times than allopatric sister pairs? (2a) Is there a history of recent colonization or re-colonization in either the generally younger, less complex, and more ecologically isolated KH montane forests, or the older and less fragmented AR or (2b) did *Hylomyscus* or *Sylvisorex* populations remain persistent and isolated in both the AR and KH regions since at least the mid-Pleistocene, before intensification of glacial cycles commenced? Although these hypotheses have clear predictions for coalescent-based parameter estimates from genetic data, predictions under hypothesis 2b can involve divergence times older than or younger than the LGM. The former case could happen if the region between AR and KH was consistently unsuitable while the latter case could occur if the region between AR and KH was suitable and occupied up until the Holocene (<15,000 Kyb) such that 2a and 2b would be indistinguishable with genetic-based divergence time estimates (Fig. 2). We therefore use a complimentary approach by combining phylogenetic inference with species distribution models (SDMs) to assess the plausibility of each species occupying the AR, KH, and intermediate areas at the LGM. An integrative approach using both genetic data and geographically explicit SDMs allows for independent testing of historical biogeographic hypotheses and can aid in recognition of evolutionary processes not apparent from genetic data alone (Knowles et al., 2007; Hickerson et al., 2010). We note that our use of SDMs projected to the LGM is not based on any *a priori* expectation of clustering of Late Pleistocene divergences, but rather because this data is readily obtainable, has been relatively well-tested, and allows detecting if any of our sampled populations may have been unsuitable during the LGM.

Our use of the term “cryptic taxa” for newly delimited clades from both genera in this study is strictly based on a lack of externally diagnostic morphological characters. As a consequence diversity in these groups has previously been underestimated. One area

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