
Review article

New perspectives on the origin and diversification of Africa's forest avifauna

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Abstract

The use of DNA sequence data in systematic studies has brought about a revolution in our understanding of avian relationships and when combined with digitized distributional data, has facilitated new interpretations about the origins of diverse clades of the African avifauna including its diversification up through the Tertiary until the present. Here we review recent studies with special reference to Africa's forest avifauna and specifically comment on the putative origins of 'hotspots' of endemism in the Eastern Arc Mountains of Tanzania and in the Cape Region of South Africa. Intriguingly, both these areas appear to have retained populations of relict taxa since the mid-tertiary thermal optimum and at the same time have been centres of recent species differentiation.

Key words: Africa, avifauna, speciation, biogeography, evolution, endemism

Résumé

L'utilisation des données portant sur la séquence ADN dans les études systématiques représente une révolution dans notre façon de comprendre les relations entre les oiseaux et, combinée avec les données numérisées sur la distribution, elle facilite de nouvelles interprétations concernant les origines de différents clades de l'avifaune africaine, y compris sa diversification tout au long du Tertiaire et jusqu'à nos jours. Nous passons ici en revue des études récentes qui se réfèrent particulièrement à l'avifaune forestière africaine, avec un commentaire spécial sur les

origines putatives des hauts lieux d'endémisme dans les montagnes de l'Eastern Arc tanzanien et dans la région du Cap, en Afrique du Sud. Curieusement, ces deux endroits semblent avoir conservé des populations de taxons résiduels depuis l'optimum thermique du milieu du Tertiaire, tout en étant aussi au centre de récentes différenciations entre espèces.

Introduction

Despite the remarkable taxonomic diversity of African birds, very limited research was conducted on their evolutionary origins and patterns of diversification between the publication of Moreau's (1966) seminal book, the first major attempt at synthesizing knowledge on the patterns of diversification in African birds, and the early 1990s. In the last two decades, the use of DNA sequence data in systematic studies has brought about a revolution in our understanding of avian relationships. For example, it has become clear that avian systematists had underestimated the plasticity of avian morphology and thus had created taxonomic groupings, which often represent functional types rather than evolutionary lineages (Barker *et al.*, 2004; Hackett *et al.*, 2008).

Molecular systematics has also helped 'discover' a number of ancient relict taxa, which had previously been 'dumped' together with phenetically similar birds of some larger taxonomic groups (see e.g. Beresford *et al.*, 2005; Fuchs *et al.*, 2006a; Johansson, Fjeldså & Bowie, 2008). Patterns of speciation in African birds, to a large extent, have been interpreted in terms of vegetational/climatic cycles during the Pleistocene, but the use of molecular data

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has formed the foundation of a debate on whether the Pleistocene caused increased speciation or the reverse (Fjeldså, 1994). Finally, the development of large digital distributional databases has greatly increased the possibility for describing the spatial variation in species richness and endemism of African birds (de Klerk *et al.*, 2002), and for analysing to what extent this can be explained from current ecology (energy, rainfall, landscape complexity; see Jetz & Rahbek, 2002; Jetz, Rahbek & Colwell, 2004). By combining phylogenetic, population genetic and distributional data, we may now begin to disentangle the relative roles of history and current ecology in shaping Africa's avifauna. Thus, the earlier descriptive biogeographical approach can give way to a search for the deeper mechanisms governing variation in biodiversity.

In this paper, we review some results of recent research with a focus on Africa's forest avifauna, and add some previously unpublished data compilations of African birds. Using these datasets, we demonstrate how certain areas (the Eastern Arc) play a central role in maintaining evolutionary processes, and we also outline our perspective on the likely 'drivers' of large-scale biodiversity patterns in Africa. Gaining an understanding of the processes, which have generated biodiversity and those that underlie its maintenance, are essential if long-term conservation goals are to be met (Moritz, 2002; Kahindo, Bowie & Bates, 2007).

The African avifauna includes most of the Old World bird families, of which most are widespread and only a few ancient groups are endemic to Africa. We abstain here from providing a complete review of families endemic to Africa because this would require extensive explanation of how the list of such groups has been affected by taxonomic revisions in progress. Instead, we direct readers to Brown *et al.* (2008) and Hackett *et al.* (2008) for nonpasserine birds, and to Barker *et al.* (2004), Beresford *et al.* (2005), Fuchs *et al.* (2006a) and Johansson *et al.* (2008) for passerine birds.

As Africa was once extensively forested, at least until the gradual aridification and spread of grasslands in the upper Tertiary (Morley, 2000; Jacobs, 2004), we assume a large portion of Africa's ancient avifauna were forest birds. Forests once covered most of northern and central Africa, from coast to coast. Southern Africa has long been arid, but the southern tip was forested during the climatic optimum in the early Tertiary. This forest formation was isolated (or possibly loosely connected to the northern forests by a strip of coastal forest) and it gradually disappeared at 39 Ma (Morley, 2000).

Fifty-eight per cent of Africa's resident birds are songbirds (Oscines), a group of Australian origin, which, according to molecular dating analyses, started their worldwide expansion right before the end of the warm early Tertiary (Ericson, Irestedt & Johansson, 2003; Barker *et al.*, 2004). A look at current distributions of species representing the deepest lineages of the songbird phylogeny could provide insights into the early diversification of this large group. As nonforest songbirds, in general, represent terminal branches, we assume that the early songbirds were associated with wooded habitats, although species that made use of oceanic islands as stepping-stones or possibly directly dispersed across the ocean (e.g. cuckoo-shrikes; Fuchs *et al.*, 2007; Jönsson *et al.*, 2008) were probably generalist insectivores of thickets and forest edges.

We evaluate to what extent the current diversity of African forest birds reflects the past history of Africa's forests. Three questions are pertinent in this context.

- 1 On the basis of the theory of niche conservatism (the tendency of species to retain ancestral ecological characteristics, Wiens & Graham, 2005), we expect the ancient forest-adapted groups to remain associated with forest, their distributions shrinking over time and their patterns of diversification following a refuge-type model where climatic cycles would lead to sequences of isolation of remaining forest fragments into refuges, while at the same time the intervening nonforest habitats expanded and provided new opportunities for radiations of nonforest groups.
- 2 Alternatively, large portions of the ancestral bird fauna were able to adapt to new niches in open habitats as their range expanded, thus maintaining large geographical distributions.
- 3 As speciation is often seen as a consequence of vicariance (the existence of closely related taxa in different geographical areas, which have been separated by the formation of a natural barrier), we would expect it to take place wherever physical barriers may lead to subdivision of ancestral gene pools; intriguingly though, much of the recent species' formation appears to be centred in specific and localized areas along certain coasts and in montane highlands such as the Eastern Arc and Albertine Rift Mountains. A central question is whether these localized centres of diversification subsequently act as dispersal centres recruiting new species to the widespread regional fauna.

Materials and methods

Distributional data for all African birds have been digitized and continuously updated for over a decade using a one-degree grid-square scale (c. 110×110 km) in WorldMap (see Brooks *et al.*, 2001; de Klerk *et al.*, 2002). This scale was chosen as a compromise between the needs for fine resolution and the poor sampling in many parts of Africa. A conservative interpolation was used where maps and satellite images suggest suitable habitat between confirmed collecting points.

For analysing historical patterns of diversification, we reviewed the published DNA-based data on avian phylogeny, and with a few examples, we illustrate how spatial and well-resolved phylogenetic data can be combined to illustrate changes in spatial patterns over evolutionary time. We assume here that the contemporary distributions of clades must reflect, to some extent, their ancestral distribution (i.e. a niche conservatism framework).

Furthermore, we provide examples from our studies of evolutionary processes operating within the remaining forest fragments of Eastern Africa, where we have had an intensive collecting program over the last 15 years with an emphasis on developing tissue, morphological and distributional databases.

Results

Patterns of species richness

Several recent studies have described the regional variation in biodiversity across Africa (e.g. Brooks *et al.*, 2001; Burgess *et al.*, 2007) including for birds (de Klerk *et al.*, 2002). As illustrated in Fig. 1(a,b) a difference exists between the diversity pattern of widespread species and those with more restricted distributions (local endemics). Jetz *et al.* (2004) convincingly argue that the former are well accounted for by current ecology (e.g. temperature, precipitation, net primary productivity, surface area) and to some extent by the expectations of a null model, which accounts for the geometric shape of the continent, whereas the more range restricted taxa follow a more aggregated pattern, which is difficult to explain from current ecology, although topography and habitat diversity play some role. Intriguingly, when the residuals from the Jetz *et al.* (2004) macroecological model are plotted on a map, they largely correspond to areas of high stability in African montane

highlands, in the Namib Desert and in the juniper woodlands of the Horn of Africa.

Historical patterns

Determining the timescale of avian evolutionary history has proven contentious, but several DNA-based studies, using different data and approaches, suggest that most of the larger groups of modern birds originated deep within the Cretaceous and survived the mass extinction at the Cretaceous–Tertiary boundary (Ericson *et al.*, 2006; Pereira *et al.*, 2007; Brown *et al.*, 2008). Much of this history may have taken place on Gondwana, and consequently much of the fossil record may be buried under the Antarctic ice. In comparison with South America and Australia, Africa does not have as many old endemic bird groups. Among these though are: ostriches (Struthionidae) of nonforest habitats, the Egyptian plover (*Pluvianus aegyptius*) of Africa's northern savannah belt (a monotypic lineage of Cretaceous age, Baker, Pereira & Paton, 2006), the turacos (Musophagidae) and the Secretarybird (*Sagittarius serpentarius*; Sagittariidae). Further, one primary clade of wildfowl must be African in origin (Crowe *et al.*, 2006), as the Numididae are restricted to Africa, and Africa is also home of the Stone Partridge and Nahan's 'Francolin' (*Ptilopachus petrosus* and *nahani*), which appear to be basal within the (otherwise American) toothquails (Odontophoridae), and *Xenoperdix* species represent a very deep branch in the Phasianidae. We consider these wildfowl species to be relictual forms, which primarily were associated with the ancient African forest, with *Agelastes* and *P. nahani* now remaining in the Guineo-Congolian forest, and *Xenoperdix* maintaining two small relict populations in Tanzania's Eastern Arc Mountain forests.

Other endemic African groups include the extant mousebirds (Coliidae), wood-hoopoes (Phoeniculidae), scimitarbills (Rhinopomastidae) and most bee-eaters (Meropidae, Marks, Weckstein & Moyle, 2007), typical rollers (Coraciidae) and honeyguides (Indicatoridae), a subclade of barbets (Lybiidae, Moyle, 2004), and the ground-hornbills (Bucorvidae) in grassland habitats, as well as the hamerkop (*Scopus*) and shoebill (*Balaeniceps*) in wetlands. The affinities of some of these lineages remain uncertain at present. However, wood-hoopoes and scimitarbills are related to the hoopoes, which in turn are related to hornbills; bee-eaters are at the base of a clade that includes kingfishers, motmots, todies, as well as typical rollers and ground-rollers which are sister to each other;

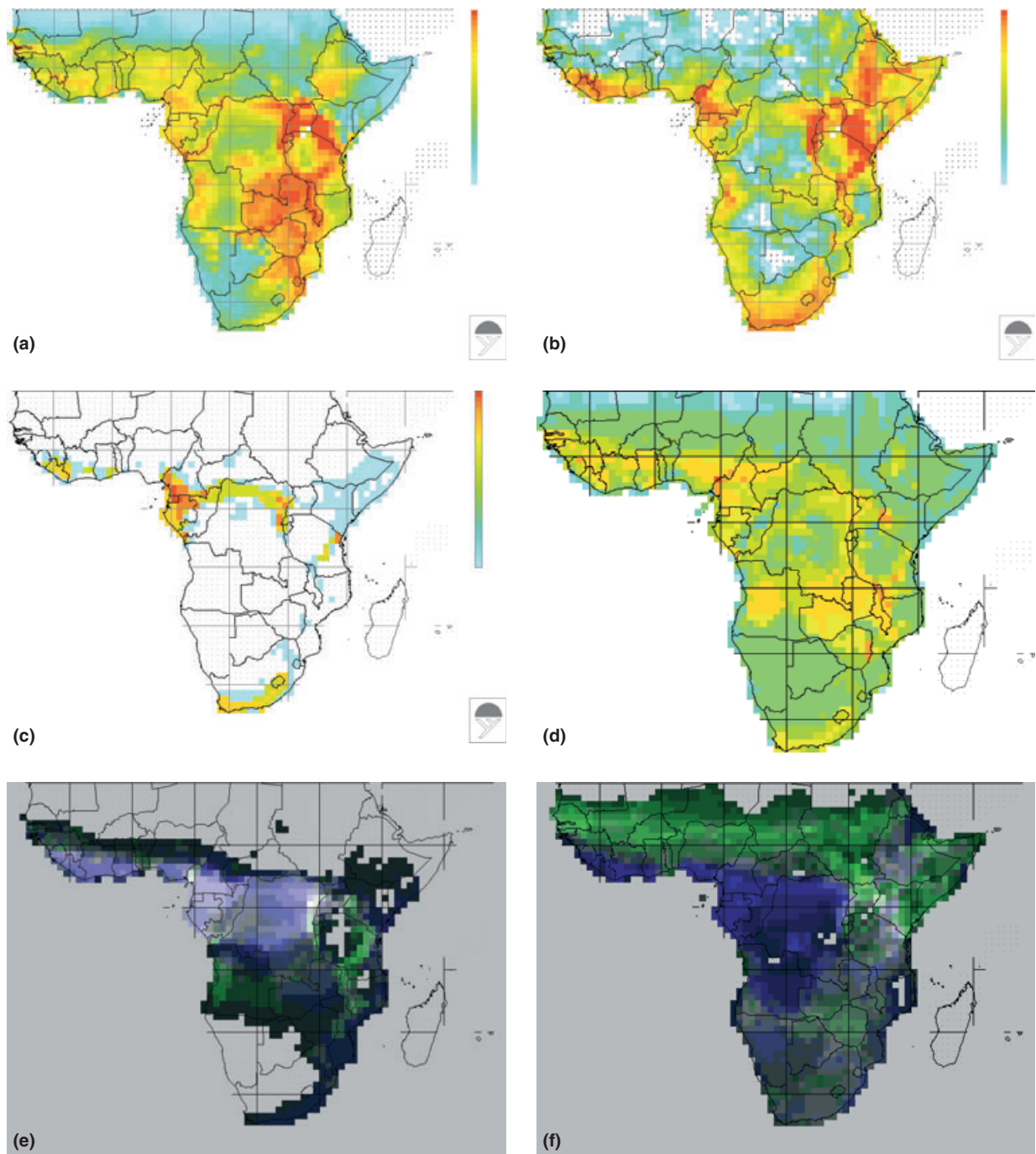


Fig 1 Large-scale patterns of avian diversity in Subsaharan Africa. (a) Species richness for widespread species (represented in >100 grid-cells) (warm colours representing the highest species counts); (b) richness of species of restricted distribution (≤100 grid-cells); (c) diversity of ancient (Eocene) relictual forms (restricted range species representing ancient and small clades); (d) richness patterns based on the present-day distribution of ten Passerida clades, which had diverged in the late Eocene; (e) diversification of greenbuls (Pycnonotidae), brightness reflecting species richness, purple colour representing 50% of the species with the shortest phylogenetic branches (=fewest steps from the root), green colour the 50% of species with longest branches; (f) diversification of glossy starlings (Sturnidae)

honeyguides are related to woodpeckers; and, intriguingly the hamerkop (*Scopus*) is now placed sister to the shoebill (*Balaeniceps*) and collectively appear to be closely related to pelicans (Hackett *et al.*, 2008). The Old World suboscines, originating in the early Eocene, may all have an African origin, with three lineages represented in Africa, namely *Smithornis*, *Pitta* and the relictual *Pseudocalyptomena graueri*, although these lineages also radiated in Asia, and recruited one species (*Sapayoa aenigma*) to the Americas (see Moyle *et al.*, 2006).

Most of the more ancient African groups are associated with woodlands. The combined species richness map for all old African clades (dating back to the warm Eocene period in accordance with various molecular dating analyses) is very similar to that for widespread species (Fig. 1a). A more restrictive mapping of only the truly relictual species, with small (<100 grid-cells) distributions and also represented by small (one to four species) old clades, recovers another pattern (Fig. 1c). This pattern is clearly different from the predictions of current environmental models (Fig. 1 in Jetz *et al.*, 2004) and instead corresponds with the traditional map of African forest refuges (e.g. Diamond & Hamilton, 1980), with peak concentrations of taxa in the Cameroon–Gabon area and the upper Congo Basin towards the Albertine Rift, and smaller aggregates in eastern Africa, notably within the Eastern Arc Mountains of Tanzania, and most surprisingly, in the Cape Floristic Region of southern South Africa.

Oscines as a special case

Because of several recent molecular studies, there is now strong evidence for an Australian origin of the oscine songbirds. With limited ability to disperse across open oceans it was initially assumed that oscines dispersed across the Wallacean Archipelago to Asia and then onwards (Ericson *et al.*, 2003; Barker *et al.*, 2004), but dispersal directly to Africa may also have been possible (Fuchs *et al.*, 2006a), considering that African oscines span the phylogeny of the oscine radiation remarkably well (Beresford *et al.*, 2005).

The phylogeny of crow-like birds (Core Corvoidea *sensu* Barker *et al.*, 2004) suggests that, in addition to dispersal through Asia there were several sweepstake dispersal events directly across the Indian Ocean to Africa (Fuchs *et al.*, 2007; Jönsson *et al.*, 2008), with these lineages now inhabiting forest and woodland habitats across Africa. Such transoceanic dispersal has also been suggested to

underpin the origins of vangas, bushshrikes and allies, which may have colonized Africa in the Oligocene (Fuchs, Fjeldså & Pasquet, 2006b), as well as for African cuckoo-shrikes, with three independent colonizations across the Indian Ocean in the Miocene (Jönsson *et al.*, 2008).

The largest clade of songbirds, the Passerida (with warblers, thrushes/flycatchers, finches etc.) must, according to their global distribution and short branch-lengths in molecular analyses, have spread and diversified extremely rapidly. Hence it has been very difficult to reconstruct their route of colonization. The discovery of several basal oscine lineages in Africa (Beresford *et al.*, 2005; Fuchs *et al.*, 2006a; Johansson *et al.*, 2008) has led to the realization that dispersal across Wallacea and then via Asia may not be the only hypothesis with which to explain the global diversification of the Passerida. As an alternative hypothesis, Fuchs *et al.* (2006a) suggested that volcanic islands in the southern Indian Ocean could have played a role as stepping-stones *c.* 40 Ma, when the global climate was still warm and the Broken Ridge of Western Australia was connected with the Kerguelen archipelago (Frey *et al.*, 2003; Fuchs *et al.*, 2006a; Jönsson & Fjeldså, 2006 for geology, and see Fig. 2).

In an attempt to illustrate the early distribution of Passerida in Africa, we superimposed the species distributions for each clade, which had diversified at 40 Ma in the late Eocene, according to the molecular data (Fig. 1d). These lineages comprise members of Sylvoidea, Muscipoidea, Passeroidea and the Paridae/Remizidae lineage (Beresford *et al.*, 2005; Fuchs *et al.*, 2006a; Johansson *et al.*, 2008), which are widespread and speciose and have been able to adapt and radiate in response to the development of dry habitats. But in addition, there are some remarkably small (relictual) groups, which were only fully recognized as a consequence of recent molecular studies: 'Picathartidae', represented in the fynbos of the Cape Region (*Chaetops*) and in tropical rainforest in Guineo-Congolian and SE Asia (*Picathartes*, *Eupetes*); 'Stenostiridae', with *Stenostira scita* in karoo scrub and montane shrubland in South Africa and Lesotho, and *Elminia* in tropical Africa (plus one genus in Asia); 'Promeropidae' (*Promerops*) in fynbos and coastal scrub; 'Modulatricidae' (*Arcanator*, *Kakamega*, *Modulatrix*) in some Afrotropical forests and 'Hyliotidae' (*Hyliota*) in tropical woodland savannahs and adjacent rainforest (Barker *et al.*, 2004; Beresford *et al.*, 2005; Fuchs *et al.*, 2006a; Jönsson *et al.*, 2007; Johansson *et al.*, 2008).

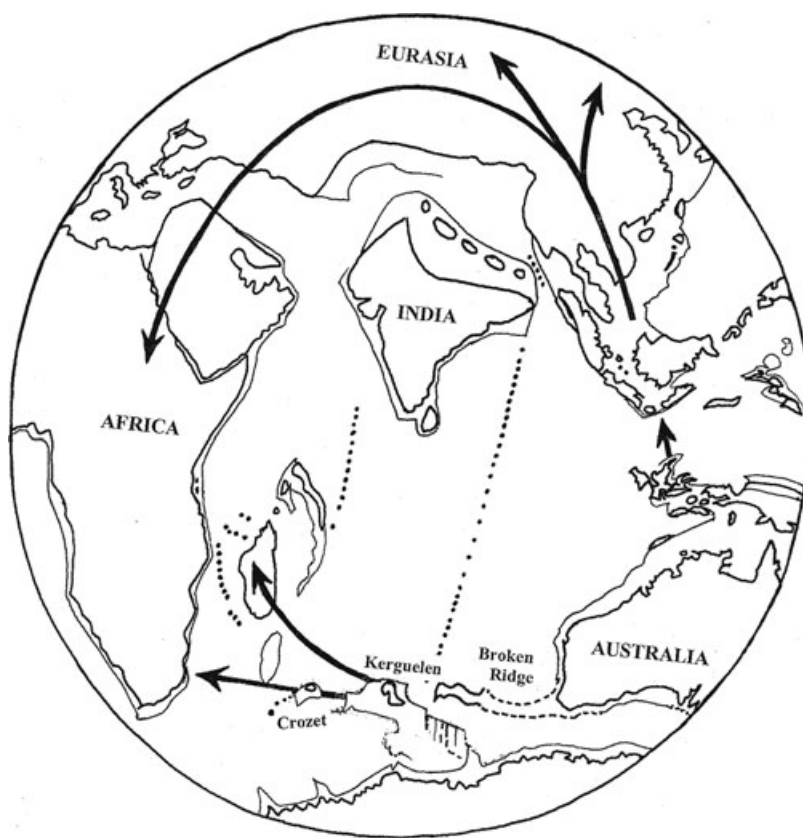


Fig 2 Land areas and continental shelf around the Indian Ocean at the end of the warm Eocene period (40 Ma) and possible dispersal routes for passerine birds (redrawn from Jönsson & Fjeldså, 2006 and updated with respect to the geological literature)

Although the two latter groups do not have representatives at the southern end of Africa, it is otherwise remarkable how well represented the ancient lineages are in the Cape Region of South Africa.

Speciation during the Neogene

Several molecular analyses now suggest a Miocene origin of most songbird lineages distributed within the primary Guineo-Congolian rainforest block (e.g. Bowie *et al.*, 2004a; Njabo, Bowie & Sorenson, 2008), with only limited divergence taking place here during the Pliocene and Pleistocene. In contrast, montane highlands and savannah regions appear to have been centres of diversification during the Plio-Pleistocene (Fjeldså, 1994; Bowie *et al.*, 2006). A significant portion of the birds inhabiting the coastal forests of the East African (Zanzibar-Inhambane) habitat mosaic are also of Miocene age (e.g. *Andropadus importunus*, Johansson *et al.*, 2007), suggesting that there were few opportunities for speciation after the connection with the wider Guineo-Congolian forest block was broken

as a consequence of rifting and tectonic uplift in Central Africa.

The forests of the Eastern Arc Mountains of Tanzania harbour a particularly large number of distinctive and medium-old species, which we regard as relict taxa: *Artisornis* tailorbirds (related to *Oreolais pulchra* and *ruwenzorii* of the Albertine Rift area, Nguembock *et al.*, 2008), *Sceptomycer winifredae*, *Malaconotus alius*, *Swynnertonia swynnertonii*, *Modulatrix stictigula*, *Arcanator orothruthus* and *Nectarinia rufipennis* among others. A similar aggregate of medium-old species is found in the Cape area and includes the *Sphenoeacus* group of warblers (Beresford *et al.*, 2005) among others.

Greenbuls, a primarily forest-adapted group, serve as an example of how phylogenetic (Johansson *et al.*, 2007) and distributional data can be linked to illustrate their diversification history (Fig. 1e). In this simplified illustration (based on Fjeldså *et al.*, 2007), the 50% of species with the shortest branch-lengths (basal lineages) are coloured in purple, the 50% with the longest branches (highest number of nodes from the base of the phylogeny, derived

lineages) are coloured in green. Both categories trace Africa's evergreen vegetation, giving a fairly high correlation between them ($\rho = 0.766$), but yet with a conspicuous difference: with the old species occurring primarily within the Guineo-Congolian rainforest, and intensive diversification occurring primarily outside it, notably in East Africa's mountains.

It should be noted that the bright green areas (Fig. 1e) correspond to peak concentrations of avian endemism in Africa (Fig. 1b), which had previously been recognized by Moreau (1966), but are now resolved in greater detail as a consequence of recent mapping projects and increased taxonomic splitting (Dillon & Fjelds , 2005).

As another example, we use Africa's glossy starlings (Fig. 1f), a primarily savannah-adapted nomadic group colonizing from Asia (Zuccon *et al.*, 2006; Lovette & Rubenstein, 2007) in rather recent times. Species representing the deepest branches are most characteristic of nutrient-poor woodland savannahs, but the group also rapidly colonized humid forests. However, the 50% of species representing the longest branches (and hence most recent speciation events) have a very different distribution ($\rho = -0.233$) in the northern savannahs and East Africa.

The Eastern Arc Mountains as a model system for diversification of montane forest birds

African montane avifaunas have traditionally been divided into seven areas of endemism (Fig. 3; Moreau,

1966; Dowsett, 1986). Although our knowledge has advanced with respect to diversification in some of these montane areas (e.g. Cameroon Mountains: Smith *et al.*, 2000; Albetine Rift: Huhndorf, Kerbis Peterhans & Loew, 2007; Kahindo *et al.*, 2007), here we focus on the Eastern Arc Mountain biodiversity hotspot (Lovett & Wasser, 1993; Burgess *et al.*, 2007) as it is better studied.

Given the extensive level of genetic structure that has been recovered within several different lineages of Eastern Arc Mountain birds (Fig. 4) and small mammals (Carleton & Stanley, 2005; Stanley & Olson, 2005; R.C.K. Bowie, W.T. Stanley & M.D. Carleton, unpublished data), it is too simplistic to recognize the Eastern Arc as a single area of endemism. Consequently, we divide the Eastern Arc into four smaller areas of endemism: (i) the northern Arc (Taita Hills, Pare and Usambara Mountains); (ii) the central Arc (Nguu, Nguru, Ukaguru and Rubeho Mountains); (iii) the Uluguru Mountains; and (iv) the southern Arc (Udzungwa Highlands), each of which has two or more endemic species restricted to them.

Generating area-cladograms for birds (Fig. 4) and estimating relative ages of divergence among adjacently distributed sister-lineages suggests that most divergence events took place well before the Pleistocene. While there is some spatial concordance among area-cladograms, there is little temporal concordance. For example, for seven of eight bird lineages studied, a genetic break is recovered between the Usambara Mountains in the

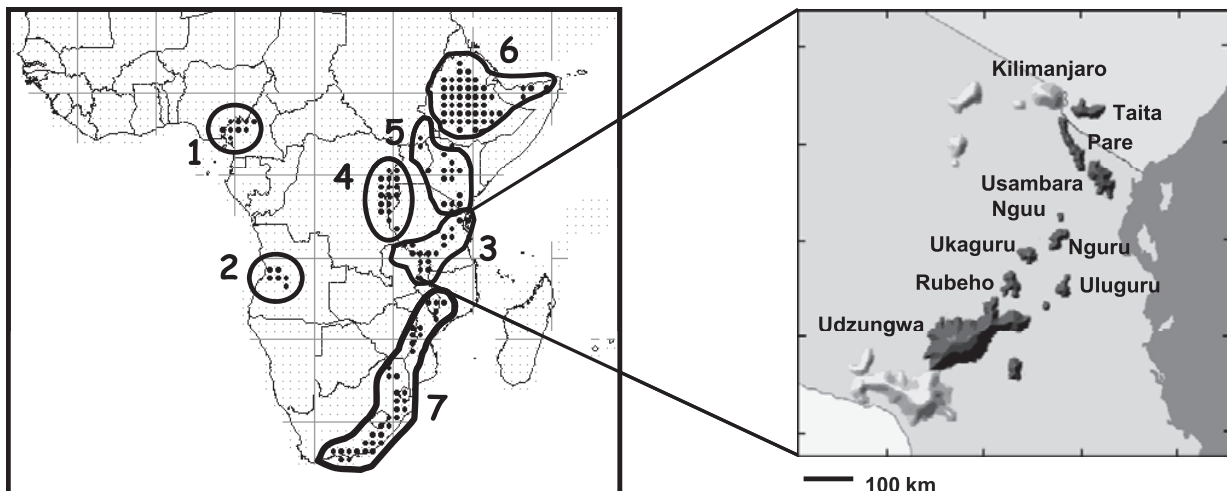


Fig 3 Left: Africa's seven traditionally recognized areas of montane bird endemism: (1) the Cameroon Highlands, (2) Angolan Highlands, (3) Eastern Arc, (4) Albertine Rift, (5) Kenyan Highlands, (6) Ethiopian Highlands and (7) the Malawi (Tanganyika) Rift and southern Africa. Right: The Eastern Arc Mountains of Tanzania shaded in black

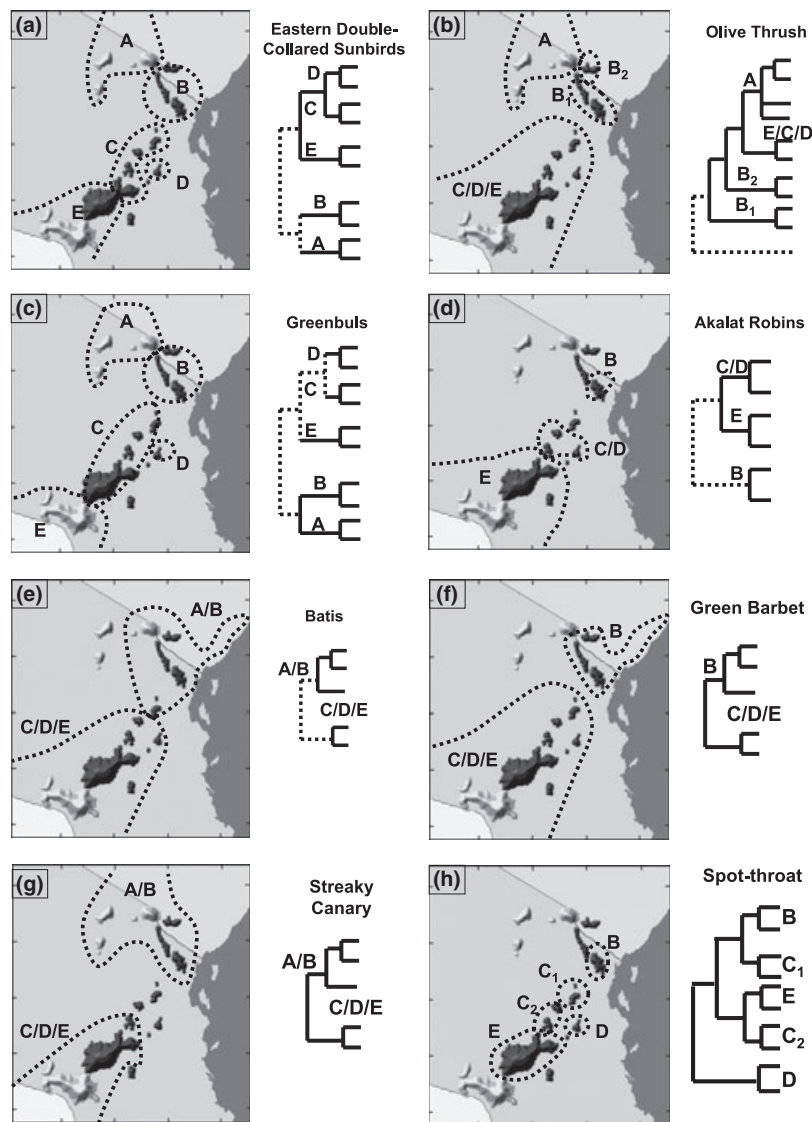


Fig 4 Area-cladograms, relationships, and estimated uncorrected-P sequence divergence (dotted lines represent branches that diverge by > 5%) among mitochondrial clades for eight lineages of Eastern Arc birds: (a) Eastern Double-collared Sunbird complex (*Nectarinia mediocris* group) – Bowie *et al.*, 2004a; (b) the Olive Thrush complex (*Turdus olivaceus* group) – Bowie *et al.*, 2005; Voelker *et al.*, 2007; (c) Greenbuls (*Arizelocichla tephrolaema* group) – Roy, Arctander & Fjeldså, 1998; Johansson *et al.*, 2007; (d) Highland Akalats (*Sheppardia montana* group) – Beresford, Fjeldså & Kiure, 2004; (e) Forest Batis complex (*Batis mixta* group) – Fjeldså, Bowie & Kiure, 2006; (f) Green Barbet (*Stactolaema olivacea*) – R.C.K. Bowie, M. Thomasset, M.J. Lawes and J. Fjeldså unpublished data; (g) Streaky Canary (*Serinus striolatus* group) – R.C.K. Bowie, E. Mostert, J.M. Bates and J. Fjeldså, unpublished data, and (h) Spot-throat (*Modulatrix stictigula*) – R.C.K. Bowie and J. Fjeldså, unpublished data

northern Eastern Arc and the Nguu/Nguru Mountains in the central Eastern Arc (Fig. 4). However, divergence estimates in mitochondrial DNA vary from 12% to 1.5% across this 110-km lowland gap: Greenbuls *c.* 12%, Eastern Double-collared Sunbird complex *c.* 10%, Akalats 7.5%, Olive Thrush complex *c.* 4.5%, Streaky Canary *c.* 2%, Spot-throat *c.* 2% and Green Barbet *c.* 1.5%. This extensive variation in sequence divergence estimates among sister clades in adjacent areas questions the validity of a purely vicariance mechanism as an evolutionary model with which to explain montane bird distribution patterns in Africa.

At an even finer temporal scale, results of population-level analyses suggest that the ancestral ranges of the Starred Robin (*Pogonocichla stellata*) and Olive Sunbird (*Nectarinia olivacea*) were fragmented in response to aridification of Africa following the cooling of the Northern Hemisphere from about 2.8 Myr BP (Bowie *et al.*, 2004b, 2006). With the retraction of ice at higher latitudes, Africa entered a wetter phase in response to the greater influence of low-latitude insolation forcing of the west and east African monsoons in relation to the Earth's Orbital precession (de Menocal, 1995, 2004). Increased precipitation and consequent expansion of montane forest may have

provided the impetus for the more recently observed secondary contact between populations in the northern and central Eastern Arc of more dispersive prone lineages (Lens *et al.*, 2002). However, even within 'dispersive' species, there appears to be evidence of lineages being isolated in the same areas of endemism as described above (Fig. 4), but within a more recent temporal (Plio-Pleistocene) framework. Intriguingly, when the haplotype network for the Olive Sunbird is examined closely (Fig. 5), it is readily apparent that the Eastern Arc haplotypes are centrally placed in a species exhibiting shallow, but significant levels of genetic differentiation across its continent-wide range

(Bowie *et al.*, 2004b). Although preliminary, the centrally placed haplotypes of the Eastern Arc (Fig. 5) hint at the Eastern Arc being the point of origin for the Olive Sunbird, from which subsequent continent-wide expansion took place. However, further studies using nuclear markers are needed for corroboration before a mechanistic explanation is sought.

Combining results from phylogenetic and population-level studies suggests that climatic cycling has had a profound influence on montane bird speciation in Africa. The results from our phylogeographic studies of Eastern Arc birds suggest that there is deep genetic divergence between

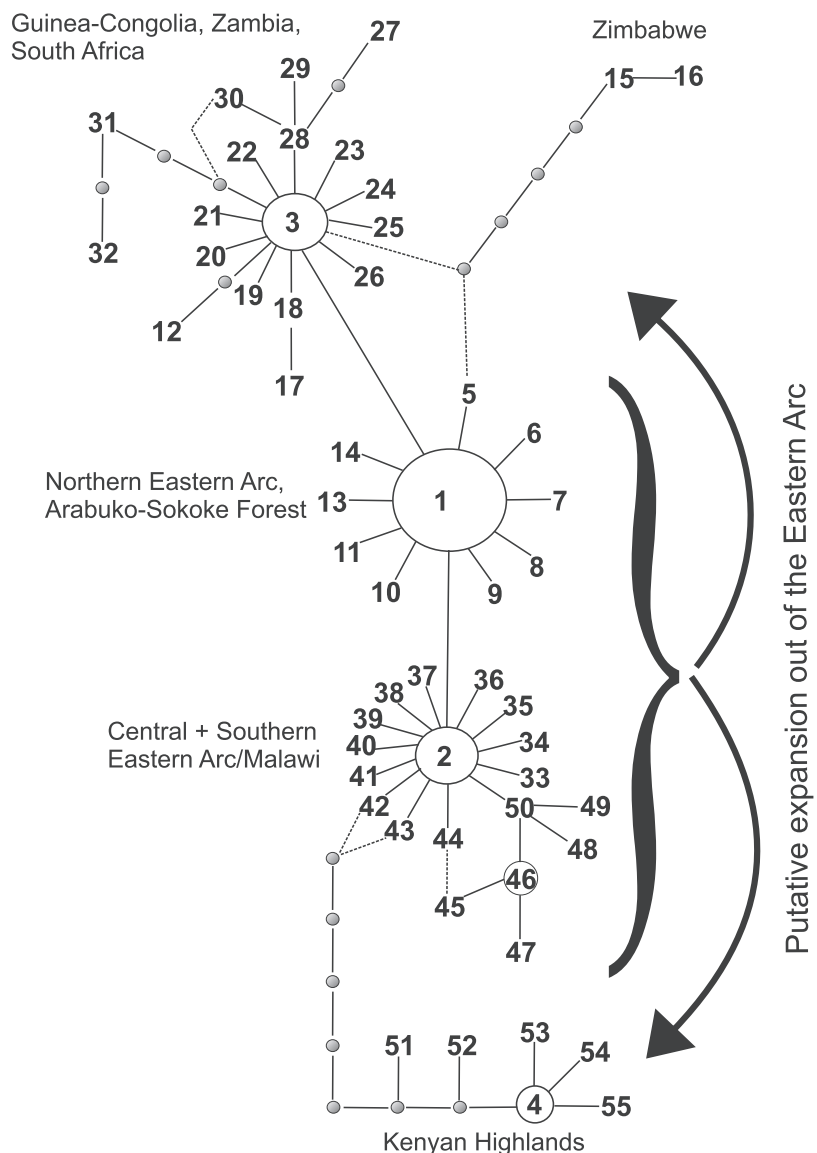


Fig 5 Statistical parsimony network of the 55 mtDNA haplotypes sampled from 282 individual Olive Sunbirds (*Nectarinia olivacea*) redrawn from Bowie *et al.* (2004b). Each line in the network represents one mutation step. Intermediate haplotypes (grey circles) are either unsampled or have become extinct

many clades (7–12%) of montane passerine birds in Africa. Generally there is support for the refuge hypothesis that isolation (fragmentation) of montane forests has facilitated speciation. However, most speciation events happened well before the Pleistocene and therefore the 'Pleistocene Refugia Hypothesis' (first applied in an African context by Diamond & Hamilton, 1980) is not appropriate as a model with which to explain general patterns of montane bird diversification in Africa. Rather, both dispersal and vicariance have played important roles in shaping montane bird communities, and the refugia type model only appears to work in the context of pulsed or cyclic expansions and contractions of montane forest, with the high peaks of endemism on certain East African Mountains (Usambara, Uluguru, Udzungwa) corresponding to lineage persistence (or lack of extinction of populations) rather than increased rates of lineage diversification. The main features of this pulsed speciation model conform to that suggested by Prigogine (1987), although the temporal dimension is wider than he hypothesized.

Discussion

The geographical pattern of relict forms contains some interesting biogeographical puzzles. While the expansion of the fynbos biome of the Cape Region is relatively young, (Verboom *et al.*, 2008) it harbours some of Africa's most ancient passerine bird lineages (*Chaetops* and *Promerops* in Fynbos, and *Stenostira* distributed further inland in the Karoo) and very few recent endemics (*Serinus*, *Nectarinia*, *Cisticola* (semi) species). Present-day distributions of ancient taxa do not necessarily reflect their past distributions, but it is tempting to assume that Fig. 1d reflects to some extent the ancestral distribution of forest birds in Africa. The large representation of early Passerida lineages in the Cape Region is in accordance with the presence of forest there in the Eocene, and with the hypothesis of colonization from Australasia via islands in the Indian Ocean (Fig. 2; Fuchs *et al.*, 2006a; Jönsson & Fjeldså, 2006) rather than via Asia. We may assume that these early songbirds survived in the south when the forest disappeared by gradually adapting to the low succulent/scrubby vegetation, and were assisted by the relative climatic stability right at the boundary between summer- and winter-rain regimes. Other elements of the ancestral austral fauna may have gone extinct, or expanded (after first adapting to nonforest conditions) so that we no longer perceive their austral origin.

As illustrated in Fig. 1(e,f), the main Guineo-Congolian rainforest acts mainly as a 'museum' where species could have persisted since the Miocene climatic optimum, but where there has been little subsequent diversification. The extent of forest cover may well have changed during the Pleistocene, but the molecular data do not suggest increased speciation rates; rather the Pleistocene climatic instability appears to have caused less lineage-sorting and hence a reduced rate of speciation (Jansson & Dynesius, 2002). One possible exception is in tropical montane areas, where local areas with more stable conditions may exist as the effect of local landscape features override the effect of climate-driven range dynamics. The Cape and the montane/forest mosaics in Tanzania are two areas characterized by high lineage persistence (locally low extinction rates), leading to accumulation of ancient lineages, as well as strong local differentiation of species representing younger radiations. At present, we are just starting to disentangle pattern from mechanism, but one aim of the research will be to determine whether within these local climatically predictable envelopes there is little directional selection and mainly neutral drift occurring, with local populations gradually becoming genetically divergent, but remain morphologically very much alike.

Conservation organizations often refer to these areas as 'biodiversity hotspots', but the term is fuzzy as its definition has drifted in time and lacks a clear biological meaning. By integrating evolutionary and macroecological approaches, we can now see the contours of a functional interpretation: 'hotspots', according to logistic regression models (Jetz *et al.*, 2004), are characterized by excessive endemism, with highly nested distribution patterns within certain low-latitude montane and coastal areas. These 'hotspot' areas may reflect intensive speciation as well as species persistence, and the spatial coincidence in certain places of old relictual forms and recently derived species suggest that both factors act in concert (Fjeldså & Lovett, 1997). This in turn suggests that endemism is primarily (based on relictual, autochthonous endemism) a consequence of special local conditions that allow populations to persist and remain stable for long periods of time, in spite of the general instability of the global climate.

We suggest, although we still have limited evidence, that African mountains with high endemism peaks (e.g. Usambara, Uluguru, Udzungwa) are places, which are inherently stable. A climatic explanation is emerging for the Eastern Arc Mountains, based on a circulation model for the Indian Ocean and is supported by a palynological

record demonstrating an absence of vegetational change during the last glacial cycle (Marchant *et al.*, 2007).

Instead of always searching for barriers to explain speciation, we need to consider also the factors that allow species to persist, often on a very local scale. Stable local areas with extraordinary lineage persistence could, theoretically, be the source for the development of co-adapted biota, and could serve as dispersal centres, as some populations start to expand with population growth (reducing the effects of genetic drift) facilitating adaptation to the more unstable regional climate. From a conservation perspective, it is essential to notice that local endemic species need not be dismissed as the 'living dead' – vanishing remnant populations in the small marginal rainforest fragments – but may instead represent a source of enrichment of the regional species pool (see also Kahindo *et al.*, 2007).

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