

Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres

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A widely accepted paradigm for speciation in tropical forests, the refuge theory, requires periodic habitat fragmentation driven by global climatic fluctuations to provide conditions for allopatric speciation. This implies that comparative species richness in refugia is due to loss of diverse communities in areas affected by climatic cycles. In this study we compare distribution patterns of bird and plant taxa which we consider to be of either deep phylogenetic lineages or recent radiations. It is demonstrated that lowland areas which have been postulated as Pleistocene refugia are dominated by species which represent lineages of pre-Pleistocene age. Since variations in species richness within these forest tracts reflect currently apparent environmental variables which might be considered to determine carrying capacity, we do not need to postulate that richness is the result of changes in forest cover in the past. Recently diversified taxa of plants and birds are found mainly at the periphery of the main rain forest blocks and in habitat islands outside them. Here, peak concentrations of young restricted-range species are often congruent with clusters of old and biogeographically relictual species. It is suggested that this reflects special intrinsic environmental properties of these areas, in the form of long-term environmental stability caused mainly by persistent orographic rain or mist. In this case, richness is not necessarily due to extinction outside these areas. Stability not only enables survival of relictual taxa, but also promotes morphological differentiation of radiating taxa, leading to aggregates of taxa of restricted distribution.

Keywords: Tropical Africa; speciation; stability; diversity; forests.

Introduction

This paper examines the hypothesis that new species evolved by isolation in forest areas which remained stable despite global ecoclimatic changes in the Pleistocene. Speciation patterns resulting from such changes, with no beginning or end phase (Haffer, 1993), would be particularly difficult to evaluate by standard methods based on the deviation and progression rules of the cladistic framework, and the basic assumption that area relationships are parsimonious. We consider that the initial step towards an evaluation could be simple comparison of superimposed distributions for large numbers of species representing distinctive evolutionary time scales. This would allow us to discover patterns which are not just reflections of the species richness, and examine whether these represent a specific evolutionary age. The impact of global climatic changes forced by Croll-Milankovitch cycles would be accentuated by a general global cooling during the last 2.8

million years, leading to large glacial peaks following the orbital precession cycles only during the last 0.9 million years (see Kutzbach and Street-Perrott, 1985; Bartlein and Prentice, 1989; Bennet, 1990; Hooghiemstra *et al.*, 1993; deMonocal, 1995; and Skinnis and Porter, 1992, for a popular review). On this basis we predict that allopatric speciation driven by climatic-vegetational cycles would be manifest mainly in biogeographic patterns of young species.

The refuge concept was first developed for South America by Haffer (1974), and was soon applied to African biota by Diamond and Hamilton (1980), Crowe and Crowe (1982), Mayr and O'Hara (1986) and Grubb (1992); see also Kingdon (1990). It was postulated that African forest-adapted species evolved by isolation in Sierra Leone-Liberia, Ivory Coast-Ghana, Cameroon-Gabon, East Zaire and East Tanzania (and maybe in levées and sumplands in the central Congo Basin, according to Prigogine, 1988) because these areas remained permanently forested during cool and arid climatic episodes of the Pleistocene.

Africa is suited to this kind of study since the modern fauna and flora was only moderately affected by tectonic change. From the mid-Cretaceous to mid-Tertiary there is no evidence of major tectonic disturbance in Africa (King, 1978), but since the mid-Tertiary, northward drift of Africa, closing of the Tethys Sea, and the central African uplift caused a gradual aridification and formation of an 'arid corridor' isolating the eastern forests from the much larger central and western forest blocks (Axelrod and Raven, 1978; Lovett, 1993a). In contrast to Africa's relatively stable geology, there is incontrovertible evidence for periodic aridity alternating with periods of raised lake levels in the Pleistocene (Livingstone, 1975, 1993; Hamilton, 1976, 1982; Bonnefille, 1983; Dupont and Hooghiemstra, 1989; Maley, 1991; deMenocal, 1995) and Holocene (Nicholson, 1994), and it has been suggested that these changes were the most important determinants of the biogeography of African forest biota (Moreau, 1966; Schiøtz, 1967; Laurent, 1973).

Although the refuge theory had paradigmatic rank a decade ago (Terborgh, 1992), and was suggested as a scientific basis for prioritising conservation areas (Brown, 1987; Terborgh, 1992), it is now being contested. It has been argued that most species of lowland rainforests predate the Pleistocene (Amorim, 1991; Hackett, 1993; Fjeldså, 1994), and a number of alternative models for diversification have been suggested (for reviews see Haffer, 1997, and Tuomisto and Ruokalainen, 1997).

As an alternative to taxon biogeography based on fully resolved phylogenies, we will compare species richness patterns representing markedly different taxonomic rank levels, and discuss species with restricted distributions, which either evolved *in situ* and failed to disperse out of the area of origin, or which are relics of previously widespread taxa (biogeographic relicts), in contrast to phylogenetic relicts, which lack close relatives, but may be widely distributed. It is our assumption that occurrence of local clusters of restricted range species which can be considered relics would reflect low rates of extinction caused by high environmental stability.

We will demonstrate in this paper that plants and birds, although they may differ considerably in terms of dispersal, spatial scales and modes of speciation, show remarkably congruent biogeographic patterns including clusters of exactly the kind suggested above. These clusters of neoendemics and relics are mainly in montane areas, or situated at the periphery of the large Congolian rain forest, and we will associate this with special intrinsic properties of these areas. We will also demonstrate that extensive lowland rain

forests postulated to include Pleistocene forest refuges were not speciation centres but acted instead as 'museums' where species (of potentially multiple origins) survived because of diversity-maintaining processes.

The conservation implications of this distinction between species richness and endemism caused by intrinsic properties of an area and diversity caused by dynamic processes acting over large geographical areas is discussed in the Editorial of this issue (Fjelds  and Lovett, 1997).

Methods

Distribution patterns of old and young species of birds and plants in Afrotropical forest were compared. In the tropics, the one-degree grid size used represents equal-area units. The phylogenetic age of bird lineages were evaluated using available DNA divergence data, while for plants biogeographical assumptions were used.

Birds representing old and recent lineages

The only dataset which reviews temporal patterns of diversification across a large taxonomic group with a uniform methodology is the vast comparative study of avian DNA by Sibley and Ahlquist (1990). These data cover the global avifauna and gives an overall measure of evolutionary divergence in altogether ca 24 000 pairwise comparisons. The data were analysed using UPGMA clustering. Despite reservations about the precise sequence and depth of nodes (O'Hara, 1991; Harshmann, 1994), for the purpose of this review we accept the relative branch lengths given by Sibley and Ahlquist (1990) as being sufficiently accurate. To minimize the impact of assumed inaccuracies we used broad categories separated by dichotomy.

The methodology for sampling deep and subordinate phylogenetic branches from the Sibley and Ahlquist data was described by Fjelds  (1994). This study lumped birds of all habitats, which limited the possibilities for interpretation. In the present review only forest birds are used, defined narrowly as those for which evergreen forest is the principal habitat. Figure 1 illustrates how old and young species were identified from a crude phylogenetic reconstruction. The DNA-based phylogenies of Sibley and Ahlquist (1990) (heavy lines in Fig. 1) were used as a framework where all modern species were inserted, based on review of published systematic revisions and phylogenetic hypotheses (see Sibley and Ahlquist, 1990; Sibley and Monroe, 1990; and Dowsett and Dowsett-Lemaire, 1993, for comprehensive references). In many cases, the topology of DNA-based trees supports morphological character transformations, which in turn helped to define in-groups and out-groups for each node of the tree. For this, voucher specimens of most taxa were examined. In order not to introduce additional assumptions about the time pattern of diversification, all nodes which are not directly supported by DNA hybridization data are regularly spaced. From all those groups where a sufficient resolution could be obtained, species representing lineages from before $T_{50}H\ 5$ ('phylogenetic relicts') and from $T_{50}H\ 5-2.5$ ('medium old species') were identified, as well as those representing a strong radiation (at least 10 species diverging above the $T_{50}H\ 2.5$ level; 'young species'). Geographical patterns of all forest species in these three categories were superimposed in Figs. 2 and 3. Distributional data are from standard reference books, national atlases and other recent publications. For classifying taxa of restricted distributions (Fig. 4), distributional data, DNA data as well as current taxonomy was used as evidence.

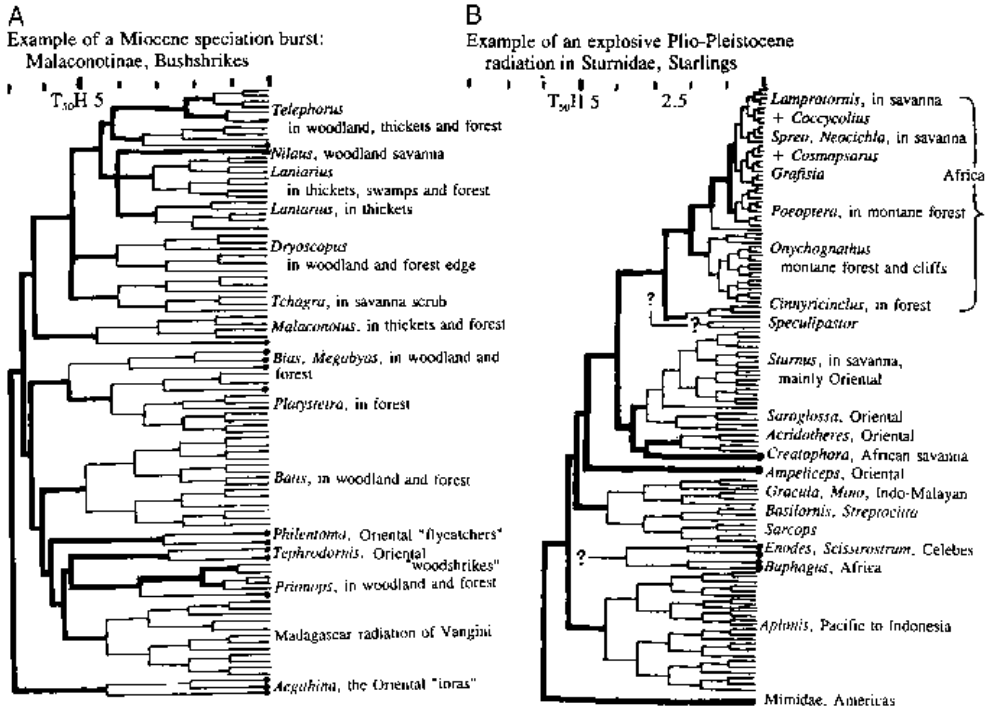


Figure 1. Phylogenetic reconstructions representing a group which radiated in the early Miocene, with slow rates of later diversification. (A) Bush- and helmet-shrikes and vangas, Malaconotinae; for earlier discussions see Meise (1968), Benson *et al.* (1971), T aylor (1970) and Sibley and Ahlquist (1990). (B) A group which first radiated mainly in the Pacific and Indo-Malayan areas and showed a rapid Plio-Pleistocene radiation in Africa: starlings, Sturnidae; revised by Amadon (1956) and Beecher (1978). T₅₀H 1.0 is assumed to correspond to ca 2.3 million years (MY) (Sibley and Ahlquist, 1990). Small, terminal solid circles identify branches identified as 'phylogenetic relicts' and 'medium old species', while curled brackets identify 'young species'.

Plants representing old and recent lineages

Phylogenetic information in the form of DNA data is sparse for plants in comparison to birds. To compare plant distribution patterns with phylogenetically old birds, genera of forest trees were selected in which the fruits are not readily dispersed and which are found west and east of the arid corridor, indicating that the generic distributions predate Miocene uplift of the central African plateau (Fig. 5A).

For comparison with young birds we used the plant genera *Impatiens* and *Crotalaria*, which are considered to form aggregates of closely related species (Fig. 5B, C). *Impatiens* is a genus of predominately shade loving moisture dependent herbs, the African species of which have been subject to a recent taxonomic revision in which 12 species aggregates were recognized containing a total of 92 species (Grey-Wilson, 1980). *Crotalaria* is a genus of herbs and shrubs which inhabit more open habitats than *Impatiens*, mainly disturbed forests, forest edge, thickets and margins of seasonally inundated areas (*dambos*). We used 237 species in groups described by Polhill (1982, Fig. 2) as 'proliferations' and excluded species referred to as 'older species' on the basis of disjunct or extra-African distributions

or distinct morphology, and the relatively unspecialised 'core species' that morphologically link species groups and subsections.

Results

Geographical patterns of birds representing deep lineages

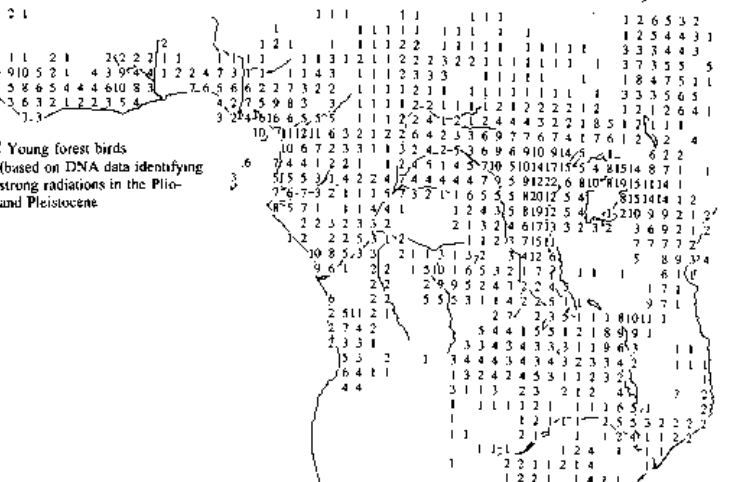
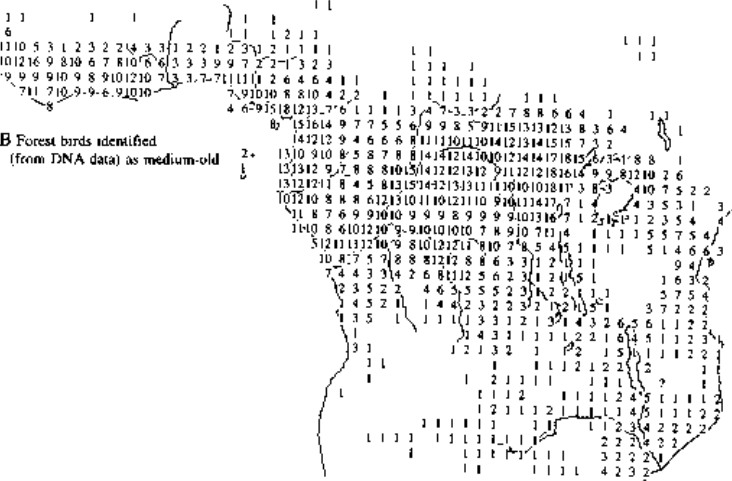
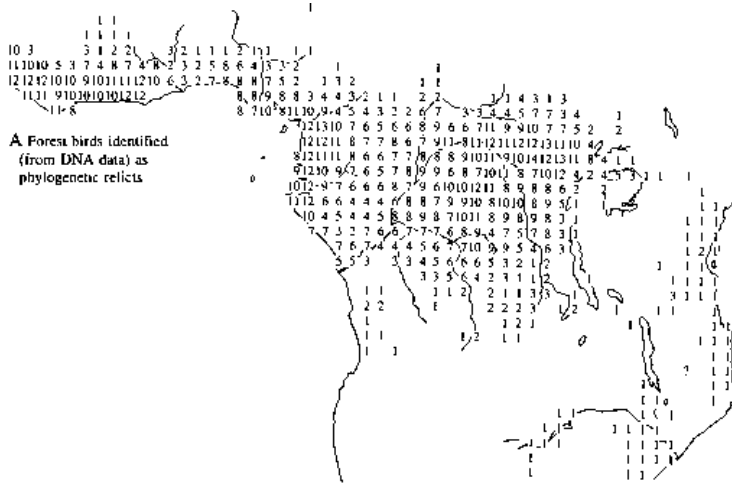
Phylogenetic relicts show a rather uniform distribution throughout the Guineo-Congolian rain forests, but with peak densities in Guinea-Liberia, Ghana, Cameroon-Gabon and the East Congo lowlands (notably Ituri Forest), with fewer species in the western part of the Congo Basin (Fig. 2A). The ancient Guineo-Congolian fauna extend across the northern Albertine Rift to the forest patches north of Lake Victoria. However, few species in this group extend to the southern part of the rifts and very few survive in the small forest fragments which remain near the east coast. The medium old species have a somewhat wider distribution, with very marked peaks in Liberia, the Cameroon-Gabon lowlands, the northern part of the Albertine Rift, and along the main rivers of the Congo Basin (Fig. 2B). A considerable number of such species inhabit East Africa, but only one species in Fig. 2B extends to the Ethiopian highlands. Other old species in this highland (see Fjelds , 1994, Fig. 4) inhabit dry thickets more than moist forest habitat.

A comparison with the overall species richness patterns of families which radiated mainly in the Miocene (forest forms of Malaconotinae, Dicruridae, Muscicapinae, Pycnonotidae and Cisticolinae sensu Sibley and Monroe, 1990) supports the pattern shown in Fig. 2A, B. However, a large number of species in these families have adapted to the woodland thickets of the savanna regions, where they are now widely distributed (see Meise, 1968). In general, the individual species have wide but sometimes patchy or even highly disjunct distributions, with some vicariance patterns, for example, across the Dahomey Gap or in Cameroon. Restricted-range species occur in the Upper Guinean Forest, in Cameroon-Gabon, in the central Congo basin, in the mountains west of the Albertine Rift and in the mountains of the Tanganyika-Nyasa group (Moreau, 1954). Those old species which inhabit the Kenya Highland are generally quite widespread and adaptable, while those inhabiting East African lowland forests comprise endemic as well as widespread forms.

Old species which are also biogeographic relicts are strongly clustered in Cameroon-Gabon and in upper Zaire (especially in the Ituri forest in the north and in the submontane zone of Itombwe forest in the south), Eastern Arc mountains of Tanzania (notably East Usambaras, Ulugurus and the eastern escarpment of the Udzungwas), with a few populations also along the Nyasa Rift (Fig. 4A) and near the Mozambique-Zimbabwe border.

Geographical patterns of birds representing recent radiations

Birds representing recent radiations (Fig. 2C) give a more 'exploded' and patchy distribution than the older lineages, with the largest concentration of species along the 'circle' of montane habitats formed by the Albertine Rift, Tanganyika-Nyasa mountains and the Kenya highlands. It is interesting to note that the density of young forest birds in the Congolian rain forest is not much higher than found in the Zambesian woodland mosaics and the Ethiopian highlands. Some moderate peaks within the Congolian block are composed mainly of disjunct populations of species with a wide total range in areas which also have many old species (and a very high total species richness, see Diamond, 1985, Fig. 1) or in specific habitats (the Ogooue and Congo deltas, Congolian riverine forest and



the sand dune forest along the Sanaga River), or at peripheral points of the Congolian forest block (Bamenda highland, Katanga scarp and East Zaire). Some close-knit species groups which can be assumed to represent Plio-Pleistocene radiations, but for which there is insufficient DNA evidence (*Columba*, *Andropadus*, *Cossypha*, *Sheppardia*, *Apalis*, certain subgroups of *Anthreptes*, *Nectarinia* and *Ploceus*) follow this general pattern. A review of all these genera shows that > 80% of the species inhabiting Congolian lowland forest also exist outside it.

Peaks which simply reflect total species richness can be removed by focusing on the young/old species ratio (Fig. 3) instead of absolute number of species. Some of the above-mentioned peaks in riverine habitats are still apparent, but young species are strongly under-represented in the Niger delta. The most prominent feature of this map is that young species dominate in mountains and at certain points at the main rain forest block margins, for example, on opposite flanks of the Dahomey Gap, in the Bamenda highlands (more than Mt Cameroon, but see Jensen and Stuart, 1985), islands off Cameroon and especially in the southern part of the Albertine Rift area. Isolated peak concentrations are found in Angola, especially in the narrow strip of cloud forest on the Amboim Escarpment (but other species are isolated in the Bailundo highlands north of the Cuanza river; see Collar and Stuart, 1985), and in woodland mosaics of Katanga and the Congo/Zambezi watershed (however, a much higher number of young species in this latter region inhabit woodland and thickets; see Fjeldså, 1994). Young species also dominate in the eastern

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Figure 2. Numbers of species of forest birds identified as phylogenetic relicts (A), medium-old species (B) and young species (C).

Phylogenetic relicts, defined as single species and a few lineages with two paraspecies, which probably originated before $T_{50}H\ 5$ (late to mid-Miocene), mostly monotypic genera, are: *Tigronis leucolophus*, *Agelastes meleagrides* and *niger*, *Afropavo congensis*, *Xenoperdix udzungwensis*, '*Francolinus*' *lathamii* and *nahani*, *Pteronetta hartlaubi*, *Himantornis haematopus*, *Canirallus oculus*, *Corytheola cristata*, *Tockus albocristatus*, '*Caprimulgus*' *binotatus* and *prigoginei*, *Pseudocalyptomena graueri*, *Picathartes gymnocephalus* and *oreas*, *Pseudochelidon eurystomina*, *Ixonotus guttatus*, *Nicator chloris* and *vireo*, *Ptyrticus turdinus*, *Arcanator orostruthus*, *Phyllanthus atripennis*, *Hemitesia neumanni*. Medium-old species, monotypic genera or aberrant species within a genus, representing a lineage arising at $T_{50}H\ 2.5-5$ (late Miocene to early Pliocene) are: *Urotrochis macrourus*, *Melichneustes robustus*, *Sasia africana*, *Tockus hartlaubi*, *camurus* and *fasciatus*, *Apaloderma vittatum*, *Ceuthmochares aenis*, *Psittacinus erithacus*, *Agapornis swinderniana*, *Gorsacius leuconotus*, *Malaconotus kupeensis* and *alius*, *Bias musicus* and *flammulatus*, *Cossypha anomala*, *archeri* and *polioptera*, *Neocossypha fraseri* and *finschi*, *Psolidoprocne albiceps* and *fuliginosa*, *Phedinopsis brazza*, *Chlorocichla flavicollis*, *Thescelocichla leucopleura*, *Urolais epichlora*, *Pseudoalcippe abyssinica*, *Modulatrix stictigula*, *Kakamega poliothorax*, *Ploceus flavipes*, *Brachycope (Ploceus) anomala*, *Parmoptila jamesoni* and *woodhousii*, *Pirenestes* spp. Young species (members of radiations with at least 10 species diverging above $T_{50}H\ 2.5$, implying that the modern species were differentiated in the Pleistocene) are: *Francolinus* (forest forms of the vermiculated and scaly groups); cuckoo-shrikes (*Campephaga*, *Lobotos*, *Coracina*, excepting two savanna forms); forest forms among African *Turdus* (*sensu stricto*); forest forms of 'glossy starlings' (*Poeoptera*, *Onychognathus*, *Cinnyricinclus*, *Lamprotornis*); forest forms of swallows (*Hirundo*, *Petrochelidon*, *Ptyonoprogne*; see Winkler & Sheldon, 1993), white-eyes (*Zosterops*, *Speirops*; omitting arid-scrub forms and the ubiquitous *Z. senegalensis*), forest forms of purple-banded and double-collared sunbirds (*Nectarinia*), canaries (*Serinus*) and the forest/woodland forms of indigofinches (*Vidua*).

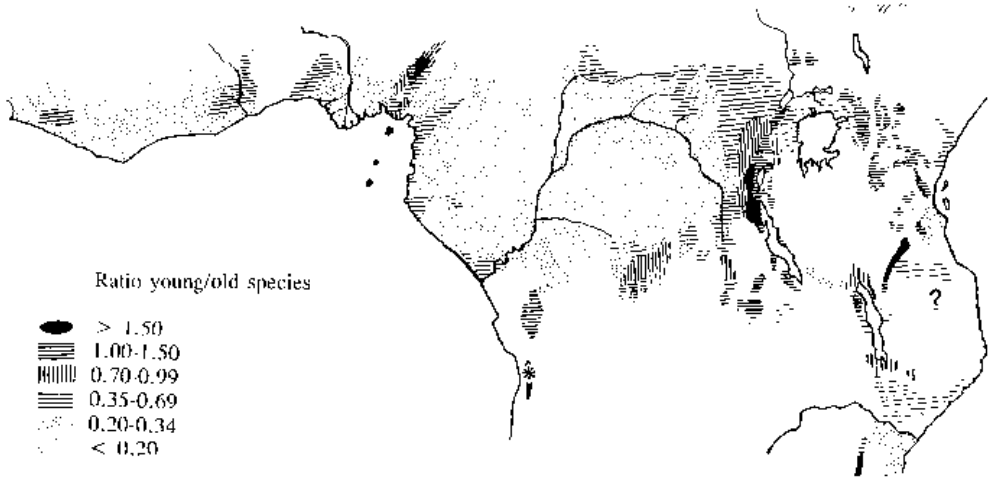


Figure 3. Geographical variation in the ratio between numbers of species in young radiations (Fig. 2C) and older species (Figs. 2A, B). Slanting lines interrupting the signature indicate that the number of species is too low for a reliable calculation.

African montane forests, while mountains near the Nyasa Rift, in Eastern Arc foothills and coastal forests have a moderate share of young species. Because of the virtual lack of old forest birds in Ethiopia, a ratio cannot confidently be calculated.

A closer examination of the East African 'circle' of montane forest habitats show that species of restricted distribution are highly clustered: peak concentrations of neoendemics (Fig. 4B) are found exactly in those mountains which also have clusters of distinctive (old) species of relictual distributions (Fig. 4A), especially the East Usambara, Udzungwa and Uluguru mountains in Tanzania. In the Albertine rift area and Cameroon-Gabon the neo-endemics peak in mountains which are adjacent to foothill forests with many old relics.

The plant dataset

The examples of old and poorly dispersed moist forest tree genera (Fig. 5A) are confined to the main Guinea-Congolian rain forest blocks and the mosaic of montane and coastal forests in Tanzania. The central Congolian forest is not well known for restricted range plants, and gaps in the map may mainly be due to variation in collecting intensity. None of the old species of forest trees extend south into the Lake Nyasa Rift or north into the Kenyan or Ethiopian highlands. Botanical phylogenetic relicts on the Ethiopian highlands are concentrated in dry thicket rather than moist forest (Friis, 1992; Lovett and Friis, in press). Concentrations of the old moist forest taxa are found in Cameroon-Gabon, the south-western part of the Congolian forests and the Eastern Arc mountains. The latter area harbours many examples of endemic relicts in a wide range of forest types, but mainly in those mountains which also have bird relicts (Fig. 4B) (Lovett, 1993b). The high rainfall area of eastern Nigeria-Cameroon-Gabon is well known to be rich in plants of restricted distribution (Brenan, 1978) with an endemic family of two species, Medusandraceae.

Impatiens shows a very low species richness in the Upper Guinean forest and in the Congo Basin, but somewhat higher numbers along the margins of the latter forest block, and marked aggregates in some of the montane areas (Fig. 5B). The highest densities of

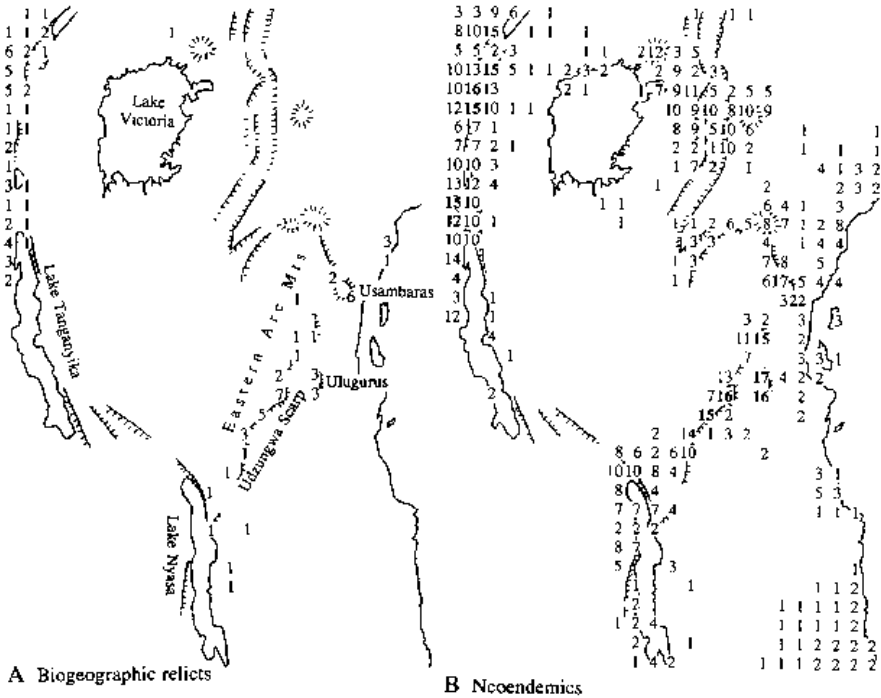
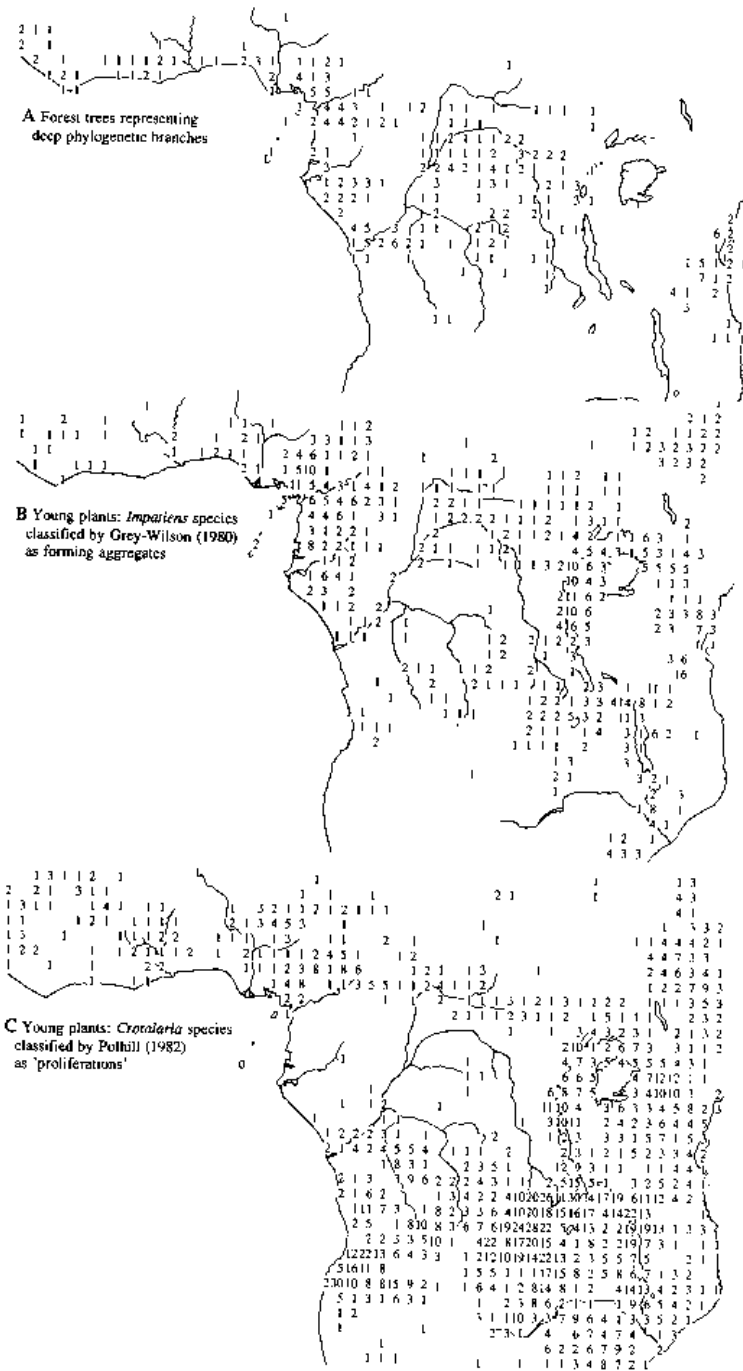


Figure 4. A comparison, for East Africa, of geographical patterns of independent (and often highly distinctive) species which show a relic distribution (A), and restricted-range vicariant taxa (phylogenetic species; range < 50 000 km²) of rapidly radiating groups.

Species defined as relicts comprise: *Afropavo congensis*, *'Francolinus' nahani*, *Xenoperdix uzungwensis*, *Himantornis haematopus*, *Canirallus oculeus*, *Phodilus prigoginei*, *Otus irenae*, *Pseudocalyptomena graueri*, *Malaconotus alius*, *Prionops alberti*, *Arcanator orostruthus*, *Swynnertonia swynnertoni*, *Hemitesia neumanni*, *Graueria vittata*, *Orthotomus metopias*, *Apalis moreaui*, *Bathmocercus winnifredae*, *Anthreptes pallidigaster* and *rufipennis*, *Ploceus golandi*.

species are in eastern Africa, on the Uluguru mountains and in the high rainfall area north of Lake Nyasa. Other concentrations are along the Udzungwa scarp, on the Usambara mountains and Kilimanjaro and Mt Mulanje (the two latter mountains lacking relicts). In central Africa high concentrations are found along the length of the Albertine Rift, especially on the western side. *Crotalaria* is similar in some respects, but is more widespread, with marked aggregates in forest/woodland/dambo mosaics on the Congo/Zambezi watershed (mainly Marungu mountains southwest of Lake Tanganyika, Lunda Plateau and other areas near Lake Mweru, northwest of Lake Nyasa and on the Angola scarp, areas which also have a number of young forest birds. The 'older' and 'core species' of *Crotalaria* inhabit lowland rainforest to a somewhat greater extent (Polhill, 1982).

Although Fig. 5A shows no peak on the western slopes of the Albertine Rift, a number of old species occur there. For example, *Impatiens briartii* which is considered to be isolated within *Impatiens* (Grey-Wilson, 1980) occurs throughout the Albertine and Tanganyika rift into northern Zambia and western Angola. A number of monotypic genera are more tightly endemic to eastern Zaire, for example *Lebrunia bushaie* (Bamps, 1970) and *Michelsonia microphylla* (Bamps, 1991). In contrast, forests in the high rainfall



area to the north of Lake Nyasa have comparatively few relicts, though the monotypic endemic shrubby genus *Temnocalyx* is an exception.

Discussion

Environmental stability and instability

The current African climate is dominated by rain originating from either the Atlantic climatic system for west and central Africa, or the Indian Ocean monsoon for eastern Africa, but with considerable orographic modification. Almost all of tropical Africa, however high the annual rainfall, has a distinct dry season (Richards, 1973) (although parts of the Uluguru mountains in Tanzania are possibly perhumid; Pócs, 1974). Within the period covered by rainfall records, the African climate has shown marked annual fluctuations in both wet and dry areas, with the climate in some places having a much greater interannual variability than others (Nicholson, 1994). Wider fluctuations are thought to have occurred in the recent past. This is the case especially with convectional local rainfall areas near the great lakes. For example, Lake Nyasa fell by at least 121 m for part of the time between the years 1390 and 1860 AD, suggesting possibly 50% lower precipitation than at present during a 330-year regression–transgression cycle (Owen *et al.*, 1990).

We will briefly review here the ecoclimatic stability of different regions of tropical Africa. The geographical pattern of rainfall variation, as demonstrated by 50 years' rainfall record (Nicholson, 1994) may be a good predictor of how different areas are affected by climatic changes also over much longer time perspectives (S. Nicholson *in lit.*; see also evidence from remote sensing by Fjeldså *et al.*, 1997). Western Africa, which lacks narrow biogeographic relicts, was characterized by anomalous events and highly unstable life zone boundaries in the Pleistocene (Dupont and Hooghiemstra, 1989; deMonocal, 1995) and has a rather variable rainfall today, except in the areas with maximal rainfall. The savanna-like 'Dahomey Gap' (2–3° East) is thought to be an effect of stochastic oceanic changes, as the cold Benguela current occasionally penetrates to the tropical coast north of the Equator (Maley, 1989). The lowlands and low mountains near the Bight of Biafra have a very high rainfall with low departures from the long-term mean; the stability extending to the savanna ecotone in the Bamenda highlands. The African west coast is unstable from the Equator to the Cape (Nicholson, 1994), but persistent mist characterizes the Angola scarp where the Benguela Current meets warm tropical water. The position of

Figure 5. Plants representing deep phylogenetic branches (A) and strong Plio/Pleistocene radiations (B, C). (A) Forest trees: *Allanblackia* (9 spp.; Bamps, 1969), *Mammea* (2 spp.; Bamps, 1969), *Zenkerella* (4 spp.; Temu, 1990), *Angylocalyx* (6 spp.; Yakovlev *et al.*, 1968) and *Scorodophloeus* (2 spp.; Temu, 1990). (B) Herbs of the genus *Impatiens*: the *I. wallerana* aggregate (9 spp.), *I. filicornu* agg. (8 spp.), *I. irvingii* agg. (4 spp.), *I. rubromaculata* agg. (18 spp.), *I. engleri* agg. (4 spp.), *I. stuhlmannii* agg. (4 spp.), *I. tinctoria* agg. (5 spp.), *I. burtonii* agg. (9 spp.), *I. kilimanjari* agg. (6 spp.), *I. gomphophylla* agg. (14 spp.), *I. hians* agg. (6 spp.), *I. macroptera* agg. (5 spp.). In the *I. filicornu* agg., the two distinctive subspecies of *I. kamerunensis* were considered separately, giving a total of 93 taxa for this analysis. (C) Herbs of the genus *Crotalaria*: the species-rich group described by Polhill (1982, see his Fig. 2) as 'proliferations' (namely the groups *Dispermae* [141 species], *Crotalaria* [15 species], *Grandiflorae* [24 species] and *Glaucæ* [57 species]).

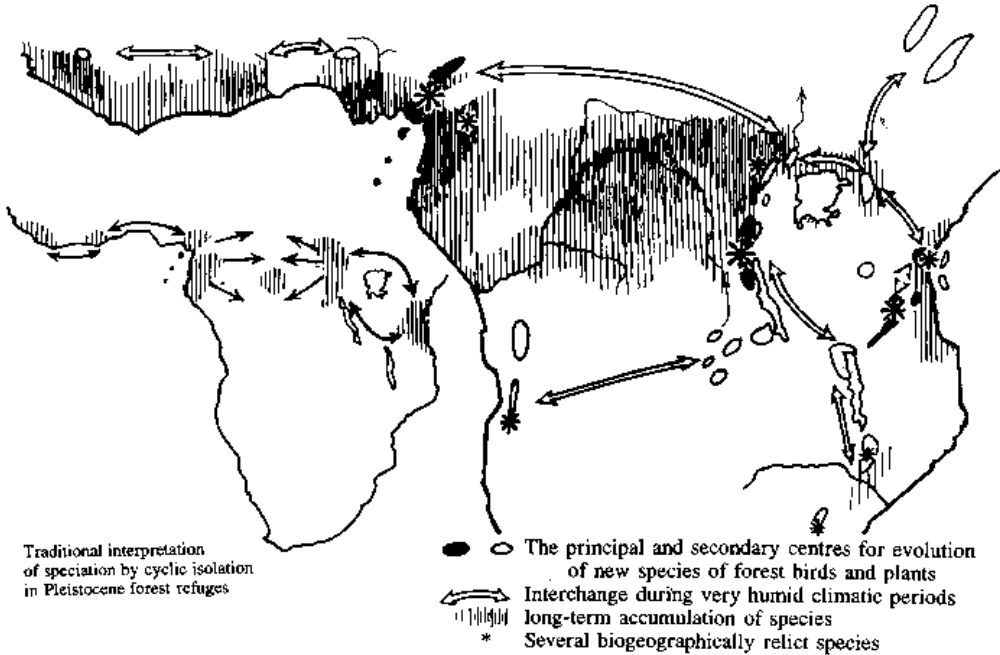


Figure 6. A re-interpretation of the spatio-evolutionary pattern for forest-adapted species in tropical Africa. The shading shows 'museums' where species of potentially diverse origins have accumulated over the upper Tertiary, with little speciation during the Pleistocene, and with the species richness patterns possibly reflecting rainfall and habitat heterogeneity. The asterisks (*) show places where the existence of several relicts indicate long-term stability, black areas centres of endemic species representing strong radiations in the Plio-Pleistocene; open areas less important centres. The insert map illustrates the earlier (traditional) concept of speciation by temporary fragmentation of the main rainforest blocks into Pleistocene forest refuges.

this front is determined by rotation of the earth, and is therefore independent of shifting climatic periods (see Best and Kessler (1995) and Fjeldså (1995) regarding an analogous phenomenon in western South America). The entire Congo Basin and Congo/Zambezi watershed are characterized by low levels of rainfall variation (Nicholson, 1994).

Eastern Africa is moderately stable, probably with the highest stability in mountains between 4° and 11°S, which are under the direct climatic influence of the Indian Ocean (Lovett *et al.*, 1988; Lovett, 1993a). Marine drill-core data suggest that the coastal waters of Tanzania were little influenced by Pleistocene climatic changes (Prell *et al.*, 1980). The East Usambara mountains are situated right at the coasts, and the Uluguru and Udzungwa mountains, although further inland, are high escarpments facing this warm and humid coast. These three points represent marked rainfall peaks in eastern Africa (Lovett, 1993c), while other Eastern Arc mountains have a lower or more variable rainfall. Forests on other highlands are influenced for part of the year by wind systems arriving over land (Kenya highlands and northern Tanzania) or related to local convectional rain arising from lakes (northern Nyasa and Rukwa Rifts).

Evidence for past climate change in Africa has been recently reviewed by Coetzee (1993), Livingstone (1993) and deMenocal (1995). It has been suggested that alternating

wet and dry periods in the Pleistocene caused cyclic isolations of forest 'refuges' and concomitant expansions of arid habitat, with the last major arid phase 14 000–21 000 years ago. However, periods of apparent climate change were not always correlated in different areas and there is a discrepancy between proposed terrestrial temperature changes and those inferred for sea surface temperatures (reviewed in Servant *et al.*, 1993). It is important to note that the existing local records of vegetational changes may reflect a number of other factors than global climatic changes. Elephants and other browsers have a conspicuous impact in savannas and forests, the former killing trees by pushing them over or by bark-stripping, the latter by suppressing saplings and keeping regeneration in the height range where they might be damaged by fire (reviewed in McNaughton *et al.*, 1993). Evidence for controlled use of fire by African hominids is at least one million years old (Brain, 1993), and there is no reason to discount a considerable hominid influence on vegetation through fire in this period. Large portions of Africa are today a plagioclimax maintained by incessant burning, and fire exclusion experiments in Zambian woodlands demonstrated that, in the absence of fire, species characteristic of moist forest regenerate in woodland (Trapnell, 1959).

Glacial moraines are problematic to use as evidence for cooler climates as their limits are not restricted to temperature changes. It is assumed that the treeline was depressed 1000–1500 m during the cold parts of the Pleistocene, but Lovett (1993a, citing D. Taylor *in lit.*) suggests that the most conspicuous effect of cold climatic periods in East Africa was restriction of the range of lowland forest and an expansion of plant communities tolerant to cool and dry conditions. However, White (1981, 1983) criticized the refuge theory formulated by Hamilton (1976), and later (White, 1993) proposed that sand deposits under the Congolian forests need not be related to aridity.

Summarizing, we will emphasize that, although certain places may remain rather undisturbed, large portions of the African forests are responding incessantly to a number of factors including cyclical climatic changes caused by orbital forcing. The resulting spatiotemporal heterogeneity will, according to disturbance regime theory (see Gilpin and Hanski, 1991) affect species composition and maintain a high regional species richness.

The lowland forests as 'museums'

The fauna and flora of those parts of the lowland rainforests which have been postulated as Pleistocene refugia are dominated by species which represent lineages of pre-Pleistocene age. Only very few cases of vicariance within the Congolian forest block are likely to represent Pleistocene events (in birds *Gymnobucco pelilsladeni*, *Illadopsis albipectus cleaveri*, and well marked subspecies of *Platysteira blissetti* and *Anthreptes fraseri*). There are few cases even in the Guineo-Congolian area as a whole, and most of these cases can be associated with special (riverine) habitats or marginal positions rather than postulated Pleistocene refugia. Thus, although we cannot exclude that global climatic changes caused contraction of the Congolian forest, there is little evidence that this caused proliferation of species. Gallery forests may maintain gene flow between isolated forest fragments. Kellman *et al.* (1994) found that savanna gallery forests can support local tree species densities that are comparable to those of continuous tropical forests in the same region, and floras that are characteristic of these forests. Even outside the normal climatic range of tropical forests, forest habitat can be maintained because of special soils, e.g. around termite mounds (Lovett and Gereau, 1990; Friis *et al.*, 1987; Abbadie *et al.*, 1992). However, this kind of forest habitat, in regions characterized by large environmental

fluctuations (maybe on any time scale) is likely to have a high species turnover and be dominated by species tolerant to a wide range of environmental conditions.

The majority of independent (old) species are widespread (Pomeroy and Ssekabiira, 1990), and could well represent lineages of adaptable species which have undergone only phyletic speciations. Willis (1922) suggested that old species are widespread because they had a long a time to reach their maximum potential ranges; this could be related to accumulated genetic plasticity.

Proponents of the refuge concept assume that species migrated between east and west when there was continuous forest, but they also cite disjunctions within the main Guineo-Congolian forest blocks as evidence of Pleistocene refugia. However, this postulate is unnecessary since the distribution of species could also be explained in terms of current carrying capacity. Many species, although able to disperse throughout the forest are only locally or sporadically present in the qualitatively poorest or least stable parts, in accordance with metapopulation theory (Levin, 1969; Pulliam, 1988; Gilpin and Hanski, 1991). It should be noted that the species richness peaks are associated with areas of very high rainfall (> 3000 mm in Guinea-Liberia, > 5000 mm near the Bight of Biafra, > 2000 mm in upper Zaire; see also Hall and Swaine, 1981, for Ghana), and that smaller peaks correspond to dynamic riverine habitats or areas with complex habitat mosaics (from north-eastern Zaire to the Kenya highland; Fig. 2). Since these patterns reflect diversity-maintaining processes which are currently apparent, we do not need to postulate that they are the result of major paleoecological fluctuations. Salo (1988) and Kalliola *et al.* (1993) give strong evidence that the exceedingly high species richness in the sub-Andean part of the Amazon Basin is maintained by fluvial dynamics and other kinds of heterogeneity in time and space (see Levin, 1992). Since evapotranspiration and habitat heterogeneity can be estimated using remote sensing data, this interpretation lends itself to statistical evaluation.

Diversification in stable places in the ecotonal regions

The few old species which have restricted and relictual distributions could represent the last remnants of past radiations. Clusters of such biogeographically relict species (Fig. 4A) fall inside high-rainfall lowland areas or specific mountains which may have predictable rain or persistent fog on ecotones towards regions often affected by drastic ecological changes. The correlation between endemism and cloud forest was documented on global level by Long (1994). It is worth noting that the Eastern Arc mountains are rich in endemic plant genera (Lovett, 1993b) and the only monotypic endemic genera of herptiles in East Africa are also in the Eastern Arc mountains, with one in the Udzungwa and one in the Usambara mountains (Howell, 1993). Some of these relics (of birds, plants and herptiles) have nearest relatives in remote areas, in western Africa, Madagascar or in the Far East (Dinesen *et al.*, 1994). Forest litter arthropods show a high single-mountain endemism throughout the Eastern Arc (Scharff, 1993).

Proliferation of young species takes place mainly at the periphery of the main rainforest blocks and in habitat mosaics outside them (Figs 2–5). Many of these species have wide distributions in forest and woodland savannas, which obscures their precise origins. Peak concentrations of young restricted-range species correlate with relict taxa (a congruence also observed in the flora of California by Stebbins and Major, 1965) or are situated in montane forests on the adjacent boundary to a savanna biome. In forest litter arthropods and herbs, which may survive for long periods in very small patches of humid habitat, e.g.

near waterfalls and in local mist zones, local 'species flocks' could probably evolve inside a limited area. Botanists often postulate a gradient (or parapatric) model of speciation in steep and complex landscapes (see Gentry, 1989; Levin, 1993; Goldblatt, 1997; however, this mode of speciation has not been evaluated using population phylogenies), or micro-geographic vicariance. New species could also be allopolyploids resulting from hybridization between different forest-inhabiting species or between species which meet on the forest-savanna ecotone (for *Syzygium masukuense*, see Lovett and Congdon, 1994) or even serial hybridizations without the parent plants being part of the present day biota. The 'species flock' of *Impatiens* in the Ulugurus could indicate micro-geographic as well as reticulate speciation. A similar 'species flock' is described for the genus *Saintpaulia*, where 10 out of 19 species inhabit the Usambara mountains (Burt, 1964; Baatvik, 1993). This genus requires very special environmental conditions, since the plants are very sensitive to drought and competition from other plants (Johansen, 1978). In the *Dispermae* section of *Crotalaria* a remarkable proliferation has taken place in the highlands along the Congo/Zambezi watershed, an area for which the complex mosaics of different habitats and ecoclimatic stability would support a similar microgeographic differentiation as suggested by Goldblatt (1996) for the African Cape. It is important to note that, on a broader biogeographic scale, such kinds of proliferation take place only in very few places, mainly in crystalline fault blocks, and not necessarily correlated with modern tectonism (confer Rosenzweig, 1995: 46–47).

In birds, the most frequent vicariance pattern in the East African montane 'circle' is to find different allospecies in the Albertine Rift area and in the Eastern Arc, or a more expanded pattern where closely related taxa replace each other in adjacent mountains, the abrupt shifts of morphotype including 'leapfrog patterns' (Remsen, 1984) where one population diverges strongly from flanking populations to either side (e.g. in *Andropadus tephrolaemus* and the bar-breasted and chestnut-throated groups of *Apalis*). The low incidence of replacements inside one montane region (*Cryptospiza*, *Nectarinia* and *Zoothera* in the Albertine Rift area) suggests that most vicariance events in birds involve isolation in different highlands rather than local speciation (see Patton and Smith, 1992, and Arctander and Fjelds , 1994, for Andean examples). Among plants, an example of a range disjunction between the Eastern Arc and Albertine Rift mountains is *Balthasaria schliebenii*; notable disjunctions between the Eastern Arc and central and west African forests are found in *Mesogyne insignis*, *Paramacrolobium coeruleum*, *Pterocarpus mildbraedii* and *Schefflerodendron usambarense*.

Following a broad biological species concept (Hall and Moreau, 1970), 18 interior-forest species are disjunctly distributed in the Albertine Rift zone and Cameroon mountains, other species being shared between the former area and Angola, or between all three areas (see Fjelds , 1991, Fig. 1; but see Dowsett and Dowsett-Lemaire, 1993, who split some biospecies into different allospecies). In those groups which normally do not leave the forest habitat, long distance dispersal between different montane areas could proceed as brief phases (during very wet climatic periods) when local populations could become established in places where the forest has the physiognomic structure of elfin forest, on ridges and scraps north and south of the Congo Basin and along the Tanganyika-Rukwa rifts (see Prigogine, 1987). Alternation between long isolations and intermittent establishment in transient habitat would add new species to the same mountain slopes.

This dynamic process differs from a traditional refuge model by associating the speciation with places with topographic relief (see Vrba, 1993), and with very specific

places (strong population bottlenecks) rather than fairly large refugia. Furthermore, it does not require visible discontinuities in the forest cover, but instead ecoclimatic instability in certain parts, where a high incidence of anomalous events leads to high turnover rates which favours widespread and adaptable species. Thus, the forest 'islands' of the Kenya highlands, although rich in species (see Fig. 2), are dominated by widespread species, the only restricted species (*Francolinus jacksoni*, *Prionops poliophus*, *Cimnycinclus femoralis* and *Zosterops [poliogastra] kikuyensis*) inhabiting shrub, *Hagenia* and *Juniperus* forest and *EricalStroebe* thickets in addition to forest. Similarly, the Kenyan highlands have few endemic forest plants, e.g. *Ixora scheffleri* subsp. *keniensis*, and *Polycias kikuyensis*. The difference in pattern between total species richness and that of restricted-range species (compare Figs 2 and 4) could, however, reflect extinction as well as speciation.

We are finally left with the question, whether the species pools of evergreen lowland forest can be built up by gradually 'absorbing' species which originated elsewhere. This cannot be properly evaluated without detailed phylogenetic studies (and even then, this idea is difficult to test). However, a review of several groups of animals and plants reveals not only vicariance between different montane areas, but also a large number of close relationships between adjacent life zones. Drier forest plants tend to have wider elevational ranges than moist forest plants (Lovett *et al.*, in press), but moist montane forest trees can descend in elevation if a niche arises (Lovett, 1996). Certain montane species have an isolated population in lowland forest or even at seacoasts (for example *Rapanea melanophloeus*; Rodgers *et al.*, 1988), and in other cases there is a closely related species in lowland forest or woodland. An apparent lowland-montane differentiation in East Africa includes the montane Eastern Arc endemic *Hirtella megacarpa*, which is ecologically separated from the coastal *Hirtella zanzibarica* (Lovett *et al.*, in press). The vanishing refuge model (Vanzolini and Williams, 1981) could serve as an explanation, but a transfer of species diversity from montane to lowland areas could also be due to higher rates of local elimination in the former, more insular habitats. Phytogeographically, montane forests have been regarded as a montane facies of lowland forests rather than an independent biome (Monod, 1957). A lack of clear elevational boundary has also been reported for spiders in the Eastern Arc forests (Scharff, 1993). All large radiations of forest birds include complex patterns of replacement between adjacent biomes (see Hall and Moreau, 1970; Crowe and Crowe, 1982; Crowe and Kemp, 1988).

To conclude, speciation in African forest biota happens in quite specific areas characterised by a considerable topographic complexity and maybe associated with special intrinsic ecoclimatic properties of these areas. The conditions, although not yet elucidated in detail, may comprise interactions between prevailing atmospheric flows, where a stable pattern of orographic rainfall or mist precipitation can be maintained despite global or local climatic changes.

A distinction between speciation centres and areas where species accumulate, or differentiate only on a broader geographic scale, has considerable implications for the conservation of biological diversity (see Fjeldså and Lovett, 1997; Fjeldså and Rahbek, in press). In the first case, very specific priorities can be made and targeted, and concentrated efforts may have a very high impact. In the second case, where the species richness is maintained by landscape dynamics acting over large geographic areas, priorities are exceedingly difficult to make, and political-macroeconomic decisions will probably have a much greater impact than any local actions.

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