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PRELIMINARY ANALYSIS OF THE NESTEDNESS PATTERNS OF MONTANE FOREST BIRDS OF THE EASTERN ARC MOUNTAINS

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ABSTRACT

Previous biogeographical studies of forest avifaunal compositions of mountains in the Eastern Arc archipelago have focused primarily on patterns of species richness and the effects of montane area and isolation. This preliminary investigation examines species composition in terms of nestedness patterns for 12 mountains in this archipelago. Twenty-eight forest species (includes five species complexes), most of which are strictly confined to the Eastern Arc Mountains, were used to evaluate the hypothesis that species composition is random with respect to nestedness. Results show that the species ordering is significantly non-random. The discussion and conclusions focus on the nested subset patterns exhibited by 14 species and, to a lesser extent, 'idiosyncratic' species and islands. Factors that may have contributed to this pattern include selective extinction and colonisation; however, further work is necessary to elucidate which of these, or other factors, actually contributes to nestedness in Eastern Arc birds. Nestedness analyses serve as an important tool to predict what species may be at risk from extinction and which islands and species require greater conservation or research attention.

INTRODUCTION

Considerable attention has recently centred on the Eastern Arc Mountains (figure 1) due to their high species richness and endemism (*e.g.* chapters in Lovett & Wasser, 1993). Deforestation of these forest 'islands', which poses a major threat to the endemic biota and overall biodiversity, has also attracted greater research and conservation attention (*e.g.* Stattersfield *et al.*, 1998).

Through the efforts of numerous scientists and conservation organisations, we have significantly more ecological and biogeographical information on the flora and fauna than two decades ago, particularly for forest birds (*e.g.* Stuart *et al.*, 1993; Dinesen *et al.*, 1994; Fjeldså & Rabøl, 1995). With regard to the Eastern Arc Mountains, three major patterns have been identified for the montane forest avifauna (see Stuart *et al.*, 1993; Fjeldså & Lovett, 1997): (i) species richness is higher in forest islands that are large and, presently as

well as historically, offer favourable climatic conditions for forest. In these areas, one to three endemic species are usually present; (ii) the montane avifauna comprises widespread African species in addition to a suite of species largely confined to the Eastern Arc; and (iii) several species are disjunctly distributed across the Eastern Arc.

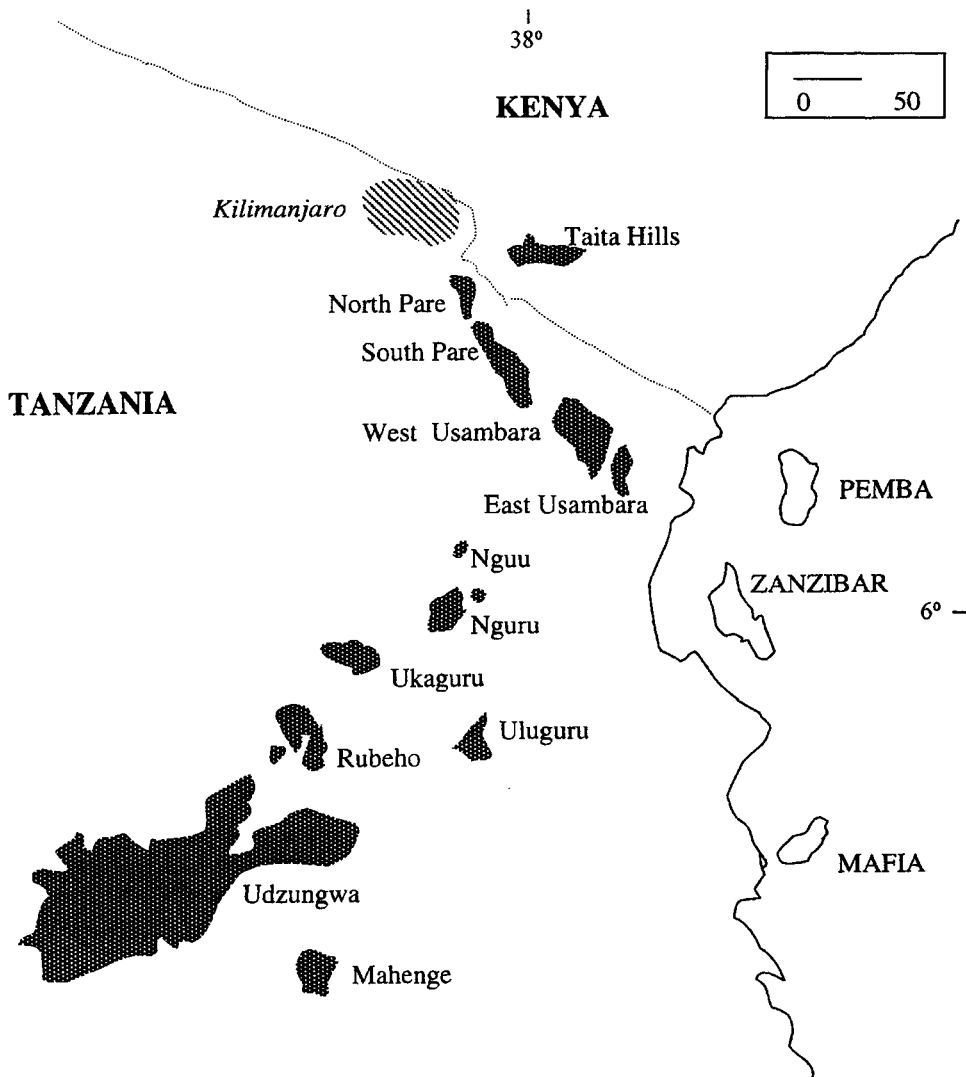


Figure 1. Map showing the locations of the Eastern Arc Mountains (adapted from Lovett & Wasser, 1993).

In an attempt to understand current distribution patterns of Eastern Arc forest birds, several hypotheses have been postulated (*e.g.* Diamond & Hamilton, 1980; Fjeldså & Lovett, 1997; Moreau, 1966). Although many of the Eastern Arc fault blocks may have resulted from tectonic activity in the Karoo Period (290–180 mya), Griffiths (1993) indicated that the current archipelago most likely developed about seven million years ago at the time when the Great Rift Valley was forming. During the early Miocene, immediately prior to the

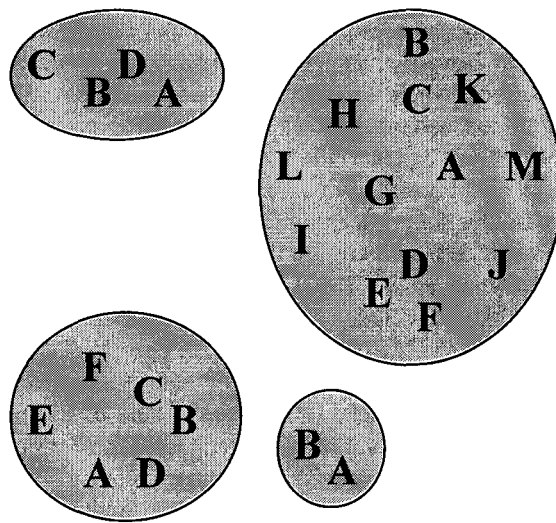
postulated formation of the Eastern Arc, forest cover was believed to have been rather widespread in much of Africa (Axelrod & Raven, 1978), but following arid to moist climatic fluctuations leading into the Pleistocene, forests became fragmented (*e.g.* Moreau, 1966; Diamond & Hamilton, 1980; Lovett, 1993). Hence, it has been proposed that over time, and especially during dry periods when forests contracted, a combination of dispersal and extinction events produced the assemblages of montane birds on each of the Eastern Arc islands (*e.g.* Moreau, 1966; Diamond & Hamilton, 1980; Fjeldså & Lovett, 1997).

Most hypotheses about biogeographical patterns of African montane birds were generally derived from qualitative studies focusing on species richness and similarity indices between montane areas (*e.g.* Diamond & Hamilton, 1980; Dowsett, 1980; Moreau, 1996; Prigogine, 1986, 1987; Stuart, 1981; Stuart *et al.*, 1993). Consequently, little attention has centred on species composition, especially in relation to possible extinction, dispersal and vicariance events (as well as other factors) that may have shaped the current distribution patterns. Given the expansion and contraction of forest due to past climatic fluctuations, and more recently habitat degradation by humans, it is crucial to know what kind of species can disperse easily and what kind are prone to extinction, and to understand how these processes may lead to the current distribution of birds in the Eastern Arc Mountains.

In this paper, I use nested subset analyses to test the null hypothesis that species composition in this archipelago is random. This analysis seems especially useful when four main assumptions are met (Atmar & Patterson, 1993): (i) that forest cover was once continuous in this archipelago and Eastern Arc montane bird species formerly occurred in all sites; (ii) all islands comprise homogenous habitats which experienced the same biogeographic history; (iii) all islands and species are equally isolated, and; (iv) there are no latitudinal effects (but see Lovett, 1996; Wright *et al.*, 1998). Furthermore, elevational effects are ignored in this analysis, but will be explored in future work (Cordeiro *et al.*, in prep.). Apart from determining the events leading to the current avifaunal distribution patterns, my preliminary analysis identifies montane areas, species and species-groups whose biogeographic patterns appear anomalous with respect to the previously mentioned general patterns.

What is nestedness?

Many authors once viewed the process of faunal relaxation, or the loss of species from a community once it becomes fragmented, as purely random; it is therefore intriguing that contemporary evidence suggests that this may not be true for most communities (*e.g.* Brown, 1971; Diamond, 1984; Patterson & Atmar, 1986). Although several scientists had earlier noted the existence of non-random extinctions (*e.g.* Diamond, 1984), it was Patterson (1984) who first identified the pattern of nestedness in small montane mammals in the western section of temperate North America. He postulated that xeric post-glacial conditions caused the once continuous boreal vegetational belts to become restricted to mountains. The fragmentation of these habitats in turn isolated small mammal populations that were restricted to these now high-elevation habitats. As habitat areas shrink, a sequential extinction process should occur whereby the same species are at risk on each of the islands, and as they disappear more quickly from smaller islands, a nested pattern should develop. If this proves to be the case, then faunas of smaller islands should technically be subsets of those on larger islands (figure 2). Nested patterns in the composition of species in progressively impoverished islands is the consequence of such ordered sequence (Patterson, 1984; Patterson & Atmar, 1986).



Nested Archipelago

Figure 2. This figure shows a nested archipelago. Species (denoted by letters) in the smaller islands are subsets of the larger ones. In a non-nested archipelago, each island may share a percentage of species with species-rich sites, but does not have an entire subset of the larger islands. For more details see Patterson (1987).

In other situations, differential dispersal and nested ecological requirements, among other factors, could contribute to a nested subset pattern (Cook & Quinn, 1995; Cutler, 1994; Wright *et al.*, 1998; Ganzhorn, 1998). What is essential for the study of nested subsets is that faunas share a common biogeographic history and today occur in more-or-less similar ecological conditions (Patterson & Brown, 1991). Although the concept of nestedness has been developed further since its inception (*e.g.* Cook & Quinn, 1995; Cutler, 1994; Patterson, 1990; Wright *et al.*, 1998), it is important to note that some authors (*e.g.* Patterson & Brown, 1991; Simberloff & Martin, 1991) believe nestedness to be near-ubiquitous and not necessarily confined to 'island' biotas.

METHODS

Nestedness

To measure nestedness of montane forest birds in the Eastern Arc mountains, I used the Nestedness Temperature Calculator (Atmar & Patterson, 1995), a windows-based program created specifically to analyse nested patterns of island biotas. This program analyses presence/absence matrices of species distribution, where islands are rows and species are columns (Atmar & Patterson, 1993). Nestedness is assessed as a 'temperature', ranging from 0–100°. A temperature close to 0° is very nested and one that is near 100° is decidedly not nested. At 100° there is no distinct pattern in the order of either species or islands (Atmar & Patterson, 1993). 'Idiosyncratic' species or sites are those that, for certain reasons, do not

follow the nestedness pattern of a given archipelago. A z-score was used to determine the probability that the 'temperatures' obtained from 1000 computer-generated simulations were different from the nestedness actually evident in the Eastern Arc avifauna.

Selection of habitat islands

Twelve Eastern Arc mountain ranges (figure 1) mentioned in Lovett & Wasser (1993) have been reasonably well surveyed and were included in this analysis (cfr table 2). There is some speculation as to whether the Taita Hills are part of the Eastern Arc range (see Brooks *et al.*, in press), but I have chosen to include this range in this analysis. To evaluate nestedness at a geographic scale, data from forests within a single mountain range have been pooled. So, for example, several montane forests in the Udzungwa range contributed records to the avifauna of the Udzungwas. Lack of sufficient data precluded analysing isolated montane forest blocks separately.

Selection of montane and Eastern Arc species

Several species found in the Eastern Arc forests that also inhabit woodland, submontane-montane and lowland forest were excluded from this analysis as the prime focus here is on the montane forest avifauna. However, the categorisation of a montane forest species is subjective given that many taxa may occur: (i) in a wide range of elevations; (ii) predominantly in highlands with satellite populations in the lowlands or vice versa; (iii) in habitats associated with forests on which they may not necessarily depend (*e.g.* Stuart *et al.*, 1993). It was difficult to assign all species as exclusively montane forest dwellers in a completely objective fashion because of these problems. The 28 taxa used here are generally believed to be restricted to submontane/montane forest in the Eastern Arc (supported by J. Fjelds , *in lit.*). By evaluating assemblages in this archipelago and assessing species as largely being restricted to the Eastern Arc montane forest, species had to have a greater part of their range in the Eastern Arc and be largely confined to submontane/montane forest to be included in this list (table 2). Elements occurring primarily in mountain ranges outside the Eastern Arc with satellite populations in bordering Eastern Arc islands were excluded from this analysis (see examples in appendix) as they may represent recent colonisers and therefore not the original suite of Eastern Arc forest birds. In future analyses (Cordeiro *et al.*, in prep.), more quantitative approaches will be used to select both montane and Eastern Arc species.

The first assumption of this analysis mentioned earlier can be easily violated if forest cover was not continuous and if the avifauna did not formerly occur in all sites. Therefore, to minimise the issue of neo-endemics that would violate this assumption, I created five species groups, which comprise closely related taxa (table 2). The taxonomy of nearly all species in these complexes remains largely unresolved (see table 2 in Fjelds  & Rab l, 1995). By creating these species groups, two Udzungwa endemics, *Serinus melanochrous* and *S. whytii* (Collar *et al.*, 1994, Stattersfield *et al.*, 1998), were placed in species complexes that largely occur in the volcanics of Kenya and Tanzania, and thus were dropped from the main analysis. Moreover, since some of these taxa are believed to be recently differentiated species, viewing them as separate units would obscure the overall nestedness pattern in this preliminary study. I did, however, examine the effects of including these 'young' species (Fjelds  & Lovett, 1997) on the nestedness pattern in this archipelago.

Sources of data

Data were obtained from the literature (see table 1).

Table 1. Sources of bird data for Eastern Arc Mountains used in this study and maximum elevation range of forest at these sites.

Mountain range	Maximum elevation (m) of forest	Sources of data*
East Usambaras	1,500	Cordeiro, 1998; Stuart, 1983, 1989
Mahenge	1,400	J. Fjeldså, <i>in lit.</i>
Ngurus	2,400	Fjeldså & Rabøl, 1995; Stuart, 1983
Nguus	1,550	Seddon <i>et al.</i> , 1995
North Pares	2,100	Cordeiro & Kiure, 1995, Fjeldså & Rabøl, 1995
Rubehos	2,050	Fjeldså <i>et al.</i> , 1997b; Fjeldså & Rabøl, 1995
South Pares	2,450	Fjeldså & Rabøl, 1995; Stuart, 1983
Taitas	2,200	Brooks <i>et al.</i> , 1998
Udzungwas	2,550	Dinesen <i>et al.</i> , 1993; Jensen & Brøgger-Jensen, 1992
Ukagurus	2,250	Evans & Anderson, 1992
Ulugurus	2,650	Svendsen <i>et al.</i> , 1995
West Usambaras	2,250	Stuart, 1983

* Data for all sites were cross-checked with the following regional publications: Britton (1980), Brown *et al.* (1982), Fry *et al.* (1988), Keith *et al.* (1992), Moreau (1940), Urban *et al.* (1986), Urban *et al.* (1997), Zimmerman *et al.* (1996).

Taxonomy

Nomenclature and systematics generally follows Britton (1980) and Zimmerman *et al.* (1996). Some deviations from this work include the consideration of several recent taxonomic splits to evaluate the effects that recently diverged taxa have on the overall nested subset analysis (see table 2 for species complexes).

RESULTS

Species richness ranges from three to 26 species for the 12 islands (figure 3). The composition of these ranges is highly nested ($T=7.95^\circ$, $p < 0.0001$) (figure 3). This indicates a strongly ordered pattern of distributions among the Eastern Arc Mountains.

To distinguish nested and idiosyncratic species, I reasoned as follows: If all species contributed equally to the nestedness of the Eastern Arc archipelago, then each would contribute equally to the temperature of the archipelago (cfr figure 3c). Unusually strongly nested and non-nested species stand out from this expected pattern as particularly short (say, half expected, or 3.98°) or especially long (say, twice expected, or 15.9°) bars. Species that fall in the middle of these extremes present ambiguities that cannot be fully explored herein. Applying this categorisation to species scores results in 14 species that were strongly nested (table 2) and five species that were distinctively idiosyncratic (figure 3c). Species that exhibited a nested pattern are divided into two main groups: (i) four are generally confined to the four mountains richest in species (figure 3b) that are assumed to have remained wet during arid conditions in the Pleistocene (Fjeldså *et al.*, 1997a) (*Xenoperdix udzungwensis*, *Apalis chariessa*, *Nectarinia rufipennis*, *Ploceus nicolli*) (ii) ten (*Bubo vosseleri*, *Andropadus milanjensis*, *Sheppardia sharpei*, *Modulatrix stictigula*, *Orthotomus metopias*, *Laniarius fuelleborni*, *Zosterops polioogastra* complex, *Nectarinia mediocris* complex, *Anthreptes*

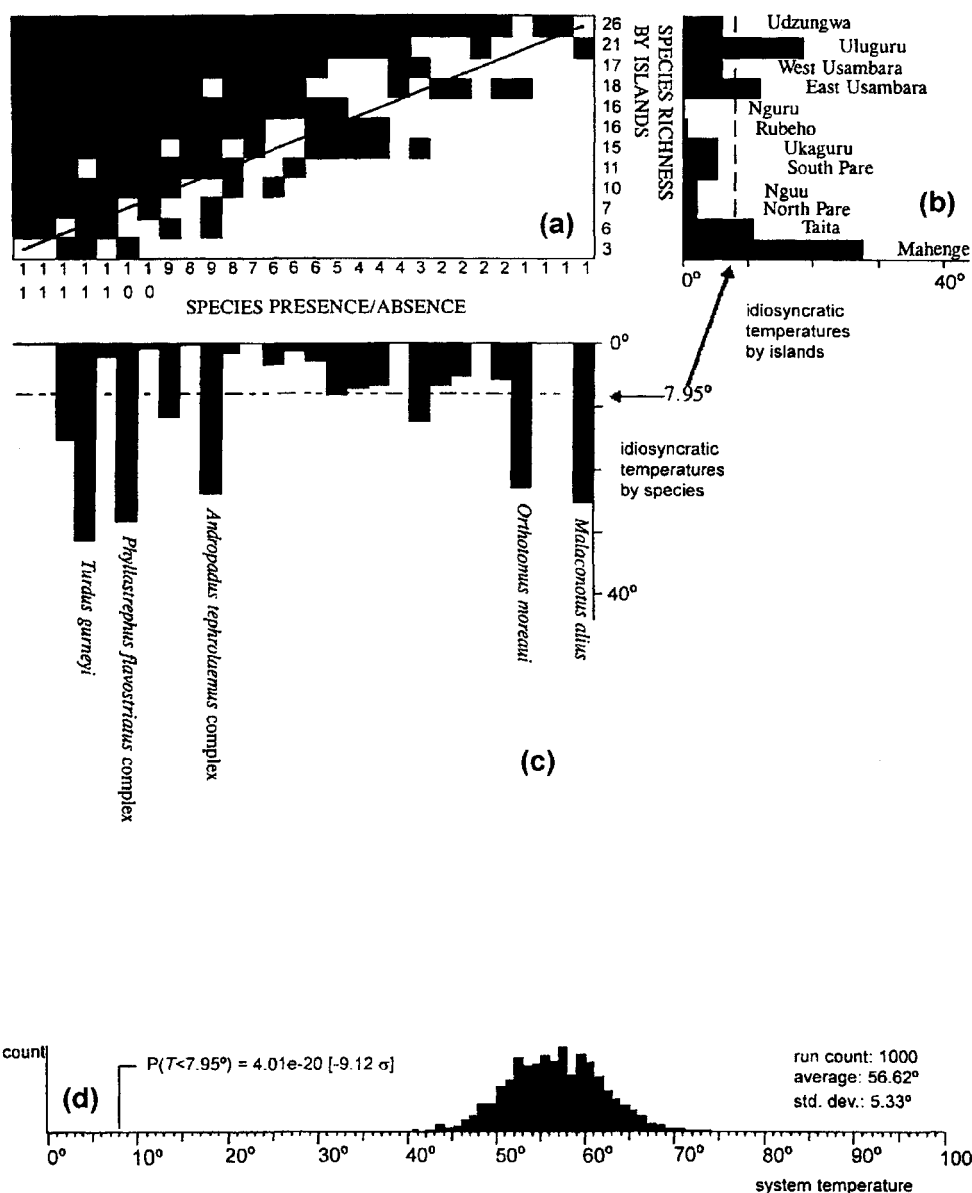


Figure 3. Nested subset patterns of Eastern Arc Montane forest birds. (a) Packed matrix showing distribution of species (columns) and species richness by islands (rows). Species presence in each island is depicted by a darkened square. (b) Nested and idiosyncratic islands portrayed here are ordered with corresponding species richness shown in (a). (c) Idiosyncratic species are listed here, whereas nested species are indicated in Table 2. Either grouping of species follows the presence/absence in the islands and therefore resulting 'temperatures' directly follow the species-island pattern shown in (a). (d) Test statistic demonstrates the highly significant nestedness pattern ($P=4.01 \times 10^{-20}$) with a 'temperature' of 7.95° .

rubritorques, *Cryptospiza reichenowi*) occur in most of the species-rich sites, ranging from six to 11 islands, but are generally absent from sites poorest in species.

Roughly a sixth of the 28 species in this archipelago exhibited pronounced idiosyncratic distributions (figure 3a, c). Two of these, (*Orthotomus moreaui*, *Malaconotus alius*) do not occur in the Udzungwas, which have the highest species richness: the first inhabits the East Usambaras, whereas the second is an Uluguru endemic. *Turdus gurneyi* is apparently absent from the South Pares, but occurs in all the other islands. On the other hand, *Andropadus tephrolaemus* complex is missing a representative from the speciose East Usambaras and maintains a disjunct distribution pattern in the species-poor sites. *Phyllastrephus flavostriatus* complex is present in Mahenge, which has the lowest number of species, but absent from the next species-poor Taita Hills (figure 3a, b, c).

With regard to islands, the most distinctively nested were the Ngurus, Rubehos, South and North Pares and Nguu Mountains whereas the second most speciose island, the Ulugurus, and the species-poor Mahenge supported relatively idiosyncratic avifaunas (figure 3b).

I also conducted the analysis viewing members of the five species complexes as separate units (table 2), including the two *Serinus* taxa mentioned earlier and *Apalis fuscigularis* and *Turdus helleri* from the Taita Hills. All of these taxa are considered as separate species by some authors (see Stattersfield *et al.*, 1998), but further molecular studies are essential to confirm these recent splits. Results of this analysis showed that the level of observed nestedness was still highly significant ($p < 0.0001$), but the temperature increased to 11.8° .

DISCUSSION

Nestedness in the Eastern Arc Mountains

Rejection of the null hypothesis indicates that the observed patterns in the distribution of montane birds in the Eastern Arc archipelago are significantly nested (figure 3d). Fourteen species and five islands strongly exhibit this pattern (figure 3a, b, c; table 2). Montane forest islands that are small in area or are located in the interior, like Taita Hills and North and South Pares contain a small subset of the more species-rich and larger sites like the Udzungwas, Ulugurus or Usambaras (see figure 1 for visual estimate of area). Both the Ulugurus and Usambaras, being more strongly influenced by the Indian Ocean, probably have remained moist under the influence of coastal rains whereas the Udzungwa scarp forest maintained wetter conditions through some of this coastal moisture as well as orographic rainfall (Fjelds  & Rab l, 1995; Fjelds  & Lovett, 1997). These generally larger montane forests, in combination with more stable climates in the Pleistocene, may have allowed more species to persist over time, being generally resilient to intense, frequent and long-term climatic perturbations.

A major hypothesis implicit in this analysis is that these mountains were formerly connected by forest, which allowed the subsequent dispersal of the avifauna between ranges. It was in the Pliocene that forest probably connected these mountains, however subsequent climatic fluctuations coupled with uplifting is believed to have isolated these mountains (see Lovett, 1993). On occasions during the Pliocene and early part of the Pleistocene, evidence suggests that at least for the latter, global cooling depressed vegetation belts and thus may have helped create lowland corridors and forest connections between mountains (see Lovett, 1993). This could indicate that most Eastern Arc birds possibly originated in or before the Pliocene, prior to the postulated earlier vicariance event. Assuming that most species

Table 2. Submontane/montane forest birds largely confined to the Eastern Arc Mountains arranged from left to right in the column order presented in figure 3b. Nested species are noted by 'n' and idiosyncratic species with an 'i'. Species of conservation concern (after Collar et al. 1994, Stattersfield et al. 1998) are marked with * in the table and, where applicable, in the notes. Nomenclature generally follows Britton (1980), Zimmerman et al. (1996), but see notes on species complexes (†).

Species	conservation status	degree of nestedness
Striped-cheek Greenbul <i>Andropadus milanensis</i>		n
Montane White-eye <i>Zosterops poliogastra</i> complex †		n
White-chested Alethe <i>Alethe fuelleborni</i>		-
Orange Ground Thrush <i>Turdus gurneyi</i>		i
Eastern Double-collared Sunbird <i>Nectarinia mediocris</i> complex †		n
Yellow-streaked Greenbul <i>Phyllastrephus flavostriatus</i> complex †		i
Red-faced Crimson-wing <i>Cryptospiza reichenovii</i>		n
Yellow-throated Woodland Warbler <i>Phylloscopus ruficapilla</i>		-
African Tailorbird <i>Orthotomus metopias</i>	*	n
Mountain Greenbul <i>Andropadus tephrolaemus</i> complex †		i
Sharpe's Akalat <i>Sheppardia sharpei</i>	*	n
Spot-throat <i>Modulatrix stictigula</i>	*	n
Banded Green Sunbird <i>Anthreptes rubritorques</i>	*	n
Usambara Eagle Owl <i>Bubo vosseleri</i>	*	n
Fülleborn's Boubou <i>Laniarius fuelleborni</i>	*	n
Chapin's Apalis <i>Apalis chapini</i>	*	-
Olive-flanked Robin <i>Cossypha anomala</i>		-
Mrs Moreau's Warbler <i>Bathmocercus winifredae</i>	*	-
Tanzania Mountain Weaver <i>Ploceus nicolli</i>	*	n
Usambara/Iringa Akalat <i>Sheppardia montana/lowei</i> complex †	*	-
Swynnerton's Robin <i>Swynnertonia swynnertonii</i>	*	-
Dappled Mountain Robin <i>Modulatrix orostruthus</i>	*	-
White-winged Apalis <i>Apalis chariessa</i>		n
Amani Sunbird <i>Anthreptes pallidigaster</i>	*	-
Long-billed Tailorbird <i>Orthotomus moreau</i>	*	i
Udzungwa Forest Partridge <i>Xenoperdix udzungwensis</i>	*	n
Rufous-winged Sunbird <i>Nectarinia rufipennis</i>	*	n
Uluguru Bush Shrike <i>Malaconotus alius</i>	*	i

Notes:

† Species complexes were formed to deal with the geographical vicariants (see table 2: Fjeldså & Rabøl, 1995). Of these complexes, *Z. winifredae**, *Z. silvanus**, *N. loveridgii**, *N. moreau** and *A. chlorigula** which are considered as separate species (e.g. Stattersfield et al., 1998) were included in the analysis which evaluated the effects of recently diverged taxa on the nestedness pattern.

- *Zosterops poliogastra* complex comprises *usambarae* (Usambara Mts), *winifredae* (S. Pares, intergrade in *N. Pares*?), *silvanus* (Taita Hills), *stierlingi* (elsewhere in the Eastern Arc).
- *Nectarinia mediocris* complex includes *loveridgii* (Ulugurus), *moreau* (Rubehos, Ukagurus, Ngurus, Ngus) and *mediocris* (elsewhere in the Eastern Arc).
- *Phyllastrephus flavostriatus* (includes *flavostriatus* in most Eastern Arc sites, but also *alfredi*, which occurs at Mahenge and is generally confined to sites outside this archipelago).
- *Andropadus tephrolaemus* includes *neumanni* (Ulugurus), *usambarae* (S. Pares, Usambaras, possibly N. Pares) and *chlorigula* (elsewhere in the Eastern Arc).
- *Sheppardia montana/lowei* represent two closely related taxa: *lowei* (Udzungwas, Ukagurus) and *montana* (W. Usambaras).

chosen for this analysis were once widespread in all Eastern Arc Mountains before the vicariance events prior to the Pleistocene, then one possibility for their modern distributions may be explained by differential extinction. Species may have been prone to extinction under the following scenarios:

- (i) Contracting forest cover due to climatic instability since the Miocene but especially the Pleistocene (Diamond & Hamilton, 1980; Lovett, 1993; Fjeldså & Lovett, 1997; Fjeldså *et al.*, 1997a), leading to 'faunal relaxation', in which extinction-prone species die off sequentially (see Diamond, 1984). This would especially be true if taxa were poor dispersers and if reduced habitat area led to eventual competitive exclusion by congeners or species with similar niches. Dispersal abilities for some species could have been too low to permit the crossing over through purported highland *Hagenia* and ericaceous scrub corridors (Fjeldså, 1994) or to sustain populations through recolonisation.
- (ii) Fragmentation of forests as a result of human activities during recent centuries. This could produce nestedness at large scales (*i.e.* when viewing the entire archipelago; Fjeldså & Lovett, 1997) or at smaller, local scales. In the case of the latter, Newmark (1991) has illustrated how habitat fragmentation can lead to the extinction of certain species in a patchwork of fragments in the East Usambara Mountains. His system was shown to be strongly nested in a later analysis by Atmar & Patterson (1995) (see also Wright *et al.*, 1998).

Patterson (1984, 1987) and Wright *et al.* (1998), amongst others, have shown that nested subset patterns commonly occur in vertebrate groups dominated by extinction events, both in habitat islands and true insular situations. In a review of nestedness among different ecological communities, Wright *et al.* (1998) point out that this pattern is strongest in land-bridge archipelagos and habitat fragments, lending support to the hypothesis that extinction events are largely responsible for many nested subsets. This may also be true in the Eastern Arc Mountains where habitat area and past climatic conditions appear to have governed the current distributions of birds. Observed nested patterns in the Eastern Arc suggest further evidence that larger forests and areas that remained climatically stable during arid conditions permitted the continued persistence of more diverse montane bird communities (Prigogine, 1987; Fjeldså, 1994; Fjeldså & Lovett, 1997). Hence, most of the species that exhibited nestedness occur in the larger and more ecoclimatically stable islands. Smaller montane forest islands and inland mountains, on the other hand, many of which lie between, or form outliers, of the Usambaras and Udzungwas, were probably affected by greater extinction and poor colonisation rates resulting from regional perturbations as described above. Nestedness in several of the islands, which generally maintain subsets of the larger and more diverse sites, could be explained by such events.

Nestedness in the South Pares is apparent but not very strong, despite being species-poor, relatively smaller in area than the other islands and having a less stable climate currently and during the Pleistocene (Fjeldså *et al.*, 1997a; Fjeldså & Lovett, 1997). This island, as well as the nearby North Pares and Taita Hills, could be impoverished due not only to unstable ecoclimatic conditions, but also local catastrophic influences such as the ash falls from Kilimanjaro's volcanic eruptions during the Pleistocene (Fjeldså & Rabøl, 1995). Moreover, the highly fragmented forest in the Taita Hills resulting from anthropogenic effects over the last few centuries most likely added to differential extinctions (see Brooks *et al.*, 1998).

Although extinction events are suggested to have influenced modern distributions of avian species in the Eastern Arc, an alternative idea is that their origins must have predated cooling episodes in the Pleistocene (ca 1.5 mya) that caused these mountains ranges to reunite. In the latter case, post-origin dispersal to neighbouring mountains would be necessary to explain modern distributions.

Colonisation was mentioned earlier as a possible mechanism that produced nestedness in the Eastern Arc avifauna (see Cook & Quinn, 1995; Cutler, 1994; Ganzhorn, 1998). Given a source island, vagile species can colonise most islands irrespective of distance, whereas moderate to poor dispersers will only be found in more accessible sites. Differential dispersal abilities can produce a strongly nested system (Cook & Quinn, 1995; Cutler, 1994; Wright *et al.*, 1998) as exhibited by, for example, land birds on islands off the Baja California coast (Patterson, 1990). Within the Eastern Arc, sites that were probably climatically stable in arid episodes of the Pleistocene like the Udzungwa, Usambara and Uluguru Mountains, may have singly or collectively (if connected via corridors) served as 'staging areas' for dispersal. This could have occurred during favourable climatic conditions in the pre-Pleistocene or in the cooling period of the Pleistocene, where forest corridors established between sites may have facilitated the spread of moderate to poor dispersers (Fjeldså & Rabøl, 1995). Where corridors were lacking, species may still have reached both nearby and remote islands if they were capable of crossing inhospitable terrain. This form of differential dispersal could explain the presence of widespread species (*e.g. Alethe fuelleborni, Andropadus milanjensis*) in most sites. Purported vagility of these two widespread species is speculative, but is supported by their cold season migrations in eastern Africa (Burgess & Mlingwa, in press). In contrast, species confined to one or two islands may be considered poor dispersers (*e.g. Modulatrix orostruthus, Orthotomus moreaui*) for a variety of reasons, including being understorey dwellers that are inhibited from crossing inhospitable terrain. Nonetheless, given our lack of sufficient knowledge on the dispersal abilities of many African forest birds, one can only speculate that colonisation may be an important mechanism that has shaped the nestedness pattern in the Eastern Arc archipelago.

Both extinction and colonisation hypotheses provide explanations of nestedness in this archipelago; an attempt to resolve the relevant importance of these two processes will be examined elsewhere (Cordeiro *et al.* in prep.). Two other factors that could play a role in nested subset patterns include habitat nestedness and passive sampling (Cook & Quinn 1995; Cutler, 1994; Wright *et al.*, 1998). In the former situation, if habitat diversity is not uniform among islands, then some islands will differentially support more species than others to produce a nested pattern. In regard to passive sampling, species that are abundant should theoretically occur on most islands whereas those that are rare may appear only on sites that harbour large numbers of individuals. Although habitat nestedness and passive sampling are potential mechanisms that could explain the nestedness pattern of montane forest birds in the Eastern Arc, discussion of these factors is deferred to a future paper (Cordeiro *et al.*, in prep.).

Finally, in their review of insular land-bridge and oceanic biota, Cook & Quinn (1995) emphasise the fact that endemic species decrease the nestedness pattern. Roy (1997) provides evidence to suggest that, at least amongst the *Andropadus* greenbuls, isolation of montane populations has led to recent speciation. Neo-endemics in the Taita Hills and South Pares may also be a result of geographical vicariance. When species complexes are subdivided to distinguish these recently diverged taxa, the level of significance remained high, but the nestedness temperature increased to 11.8°. 'Young' species arising from differentiation

through isolation in some of the outliers (Fjeldså & Lovett, 1997) therefore complicate the overall nested subset pattern.

Clues offered by idiosyncratic species and islands

Of the five strongly idiosyncratic species, *Orthotomus moreaui* and *Malaconotus alius* are found in the Usambara and Uluguru Mountains, respectively, but not in the most diverse Udzungwas. Studies on the autecology of these birds are probably essential for understanding their peculiar distributions. Possibly, specific conditions permitting the survival of these two species are present in the Usambaras and Ulugurus and may be absent from the other islands. With respect to *Turdus gurneyi*, apparent absence from the South Pares has contributed to its idiosyncrasy. Given its widespread distribution in this archipelago, it is remarkable that several surveys have missed this bird there. Perhaps long-term surveys of unexplored areas in the South Pares will find it there. As to the *Phyllastrephus flavostriatus* complex, inclusion of the form *alfredi* (largely distributed outside the Eastern Arc) introduces it to Mahenge, which is the poorest site, and not the two northern species-poor islands. In contrast, *Andropadus tephrolaemus* complex differs in that representatives are not known from the East Usambaras and Nguus, both of which probably lack sufficient montane forest (cfr table 1) to support populations of this species complex.

With regard to sites, the idiosyncratic Ulugurus, despite being between the Udzungwas and East Usambaras, do not have three species that these other two mountains share (*Swynnertonia swynnertoni*, *Modulatrix orostruthus*, *Anthreptes pallidigaster*) nor a few more that are known from each mountain range. The absence of these species from intervening sites like the Ulugurus could suggest that these birds may be especially poor dispersers. Hence, after colonising the northern extreme during favourable conditions, isolation in combination with inhospitable terrain might have limited their dispersal, thereby lowering recolonisation rates in the wake of local extinctions. Dry phases and reduced forest connections in the past, along with lower dispersal capabilities, competition and localised extinctions (see Diamond, 1984) may have limited populations to these mountains. An alternative explanation for this peculiarity, especially for *S. swynnertoni* and *A. pallidigaster*, is the lack of suitable lowland/submontane forest habitat in areas between their montane distributions.

Mahenge is highly idiosyncratic in comparison to other islands. Not only does it lack some of the widespread species, but also it harbours three species that are generally absent from other species-poor sites. The presence of *Alethe fuelleborni*, *Phyllastrephus flavostriatus* complex and *Turdus gurneyi* in Mahenge can be attributed to the presence of suitable habitat, chance, or high vagility. The lack of widespread species on Mahenge could be due to a variety of reasons. Since Mahenge is lower than its neighbours (see table 1) it probably does not have sufficient source submontane forest habitat to support many of these montane elements. Alternatively, forest corridor connections between Mahenge and Udzungwas may have been present during favourable climatic conditions to have allowed for the dispersal of forest birds.

Conservation benefits of nestedness studies

In nested systems, smaller islands support the more widespread and abundant species, but do not support narrowly distributed forms (Patterson, 1987). Thus, if there is a direct correlation between large habitat size and high species richness, more extensive areas (in which extinction rates are generally lower; Diamond, 1984) would be most important to conserve, as both common and rare species occur in such sites (Patterson, 1987; 1990). This

is manifest in the Eastern Arc where the bulk of endemics and near-endemics occur in the more speciose Usambara, Udzungwa and Uluguru mountains. If we consider recently diverged taxa, as Stattersfield *et al.* (1998) have chosen to, then important islands for species conservation should also include outliers like the Taita Hills and South Pares (both containing neo-endemics).

Although it is logical to conserve larger forested areas, it is important to pay attention to the high rate of human-caused deforestation across many of the smaller forest islands, which may hold remnant populations of rare species. If linked by colonisation corridors, some smaller islands may be part of metapopulations for such species, whereby emigrating and immigrating from island to island could slow or reduce extinction rates (Stacey *et al.*, 1997). This, of course, would depend on dispersal abilities of species, a phenomenon that has not received much attention with respect to mainland African forest birds. In general, however, greater conservation attention has centred on species believed to have poor dispersal abilities and are thus globally or regionally restricted to a handful of sites, making their conservation priorities higher in comparison to more vagile species. Sustaining overall biodiversity should therefore be a two-fold process: (i) centring on isolated taxa and (ii) focusing on how the colonisation process of birds in different islands could be enhanced by protecting more islands or fragments. Furthermore, some of these smaller islands could be critical stepping stones for some species and thus eliminating such habitats could reduce necessary gene flow between populations.

Of the five species showing distinctively idiosyncratic distributions, two species and two taxa within the *Andropadus tephrolaemus* and *Phyllastrephus flavostriatus* complexes are of conservation concern globally (Collar *et al.*, 1994; Stattersfield *et al.*, 1998) (table 2, cfr figure 3c). Several ideas have been proposed to explain the general and localised patterns for these idiosyncratic taxa. It is clear that for most, detailed autecological studies are required to determine what abiotic and biotic factors are responsible for their patchiness. In addition, the absence of some of these species could very well be due to short survey efforts and more long-term or bi-seasonal investigations are warranted. The Nguus, North and South Pares, Rubehos, Ngurus and Mahenge have generally been neglected and although their low species richness may be real, there is always the chance of yielding new discoveries (*e.g.* recent observation of an Usambara Eagle Owl *Bubo vosseleri* in the South Pares by T. Romdal per J. Fjeldså, *in lit.*).

Finally, the observed nested subset patterns in the Eastern Arc montane forest birds are likely to apply to other animal groups. Birds are generally considered to have considerable dispersal abilities and have, in this case, demonstrated pronounced nestedness. Perhaps an evaluation of animal groups that are less vagile may indicate similar or different patterns. Such studies may be important in understanding the overall biogeography of the Eastern Arc Mountains. From a conservation standpoint, species and forest islands requiring further investigations could be identified through their idiosyncratic distribution patterns.

CONCLUSIONS

Montane forest birds whose distributions centre in the Eastern Arc exhibit a nested subset pattern. This indicates that the species ordering in this archipelago is due to non-random events, which probably can be attributed to the unstable climatic conditions in the past. It is possible that most Eastern Arc birds originated prior to vicariance events leading into the Pleistocene that are believed to have separated fauna on these mountain ranges.

Alternatively, most Eastern Arc birds may have originated before the cooling period in the Pleistocene, which probably connected forest islands and therefore their current distributions may be a result of post-origin dispersal from a source site(s) after this event. Whether Eastern Arc birds were present on all montane islands before the Pleistocene or during the Pleistocene, several explanations can be sought to interpret the nested subset pattern in this archipelago.

Dry periods that caused once connected forests to become isolated may have led to a deterministic order of extinctions due to ecological instability, competitive exclusion or other factors. Coupled with this is the loss of forest cover due to human activity, which may also have contributed to the observed pattern. Thus the smaller or less climatically stable montane forests do not have a certain group of species whereas the larger and climatically stable areas sustained larger communities and many of the rarer species. Extinction events may be an important factor in avian distributions of this system; however, differential colonisation from source sites through the establishment of forest corridors connecting some of the montane forest islands could well have contributed equally to this pattern. Other factors such as habitat nestedness and passive sampling, although discussed to a limited extent in this paper, could be alternative explanations for nestedness in the Eastern Arc avifauna. Although this study is still in the provisional stage, the remaining questions to be considered may offer some important insights regarding the biogeography, ecology, evolution and conservation of Eastern Arc birds.

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