



Elevational zonation of afrotropical forest bird communities along a homogeneous forest gradient

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ABSTRACT

Aim This study analyses the distribution and abundance of birds from a forested tropical gradient in order to determine whether elevationally distinct communities are detectable in this habitat.

Location An avifaunal census was carried out on a single transect within the tropical forest of the Udzungwa Mountains in the Eastern Arc, Tanzania, covering a range in elevation from 300 to 1850 m.

Methods Two complementary data sets on forest birds were analysed, encompassing (1) data derived from standardized 20-ha spot-mapping censuses performed at nine elevations over 175-m intervals from 400 to 1800 m a.s.l., and (2) all observations of birds binned into 32 data points at 50-m intervals, from 300 to 1850 m a.s.l. The degree of zonation in the avian community along the elevational gradient was examined using the chronological clustering method, an agglomerative hierarchical clustering method that can be carried out with a range of similarity indices.

Results The chronological clustering analysis of the data set based on standardized spot-mapping revealed a clearly defined boundary at c. 1200 m a.s.l., separating lowland from montane communities. Most bird species could be categorized as belonging to one of these two communities. The data set based on all observations revealed a number of potential secondary boundaries, although these boundaries delimited the entire elevational ranges of individual species in only relatively few cases.

Main conclusions In contrast to previously published studies, we find evidence of an elevational zonation of distinct communities within a seemingly homogeneous habitat. Although similar boundaries have been assumed to arise as a result of vegetational ecotones, or because of interspecific competition, these mechanisms are poorly corroborated. We suggest that the causes of patterns of zonation are not well understood, and that the interplay among species distributions, species richness, and environmental factors needs more consideration. The chronological clustering method is proposed as an appropriate tool for studying these specific patterns.

Keywords

Africa, birds, chronological clustering, Eastern Arc, ecotones, elevation, species turnover, Tanzania, zonation.

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INTRODUCTION

Elevational gradients continue to present a specific challenge for the understanding of basic ecological patterns. After a

century of research, the variation in patterns of elevational species richness, and the causes thereof, are still not well understood (Lomolino, 2001; Rahbek, 2005). The question whether species assemblages are elevationally structured

constitutes another expression of the same conundrum, as a change in species richness by definition implies turnover of species (Rahbek, 1997; Mena & Vázquez-Domínguez, 2005).

There has been a recent revival of interest in the analysis of elevational zonation (Orlóci & Orlóci, 1990; Cornelius & Reynolds, 1991; Hofer *et al.*, 1999, 2000; Kessler, 2000b; Hemp, 2002; Tuomisto *et al.*, 2003; Mena & Vázquez-Domínguez, 2005). Studies on tropical elevational gradients have traditionally been descriptive (e.g. Terborgh, 1971, 1977; Fjeldså & Lovett, 1997; Patterson *et al.*, 1998), and there has been a lack of rigorous analyses of zonation on local transects (but see Hofer *et al.*, 1999; Herzog *et al.*, 2005; Mena & Vázquez-Domínguez, 2005), whereas ecotones in general have been proposed on the basis of simple clustering or ordination methods (e.g. Beals, 1969; Pendry & Proctor, 1997; see also the review in Odland & Birks, 1999). Given this paucity of statistically based analyses, R. H. Whittaker's classical question regarding the elevational structure of assemblages (Whittaker, 1967) remains essentially unanswered; that is, are ranges arranged in one of four models: (1) sharply defined, mutually exclusive communities, (2) mutually exclusive species pairs lacking community structure, (3) distinct communities with broad zones of overlap, or (4) random patterns of distributions?

As with any other aspect of species distribution, individual elevational ranges cannot be random *per se*, but must be the result of a plethora of biotic and abiotic factors, including historical factors, that shape the populations of the individual species (Kessler, 2000a; Colwell *et al.*, 2004; Cardelus *et al.*, 2006). Nevertheless, when observing an entire assemblage of distributions, the emerging higher-level pattern can be indistinguishable from randomness (Whittaker, 1967; Colwell *et al.*, 2004). Although many factors influence elevational distributions, it has been proposed that only species/community interactions should lead to model 1 zonation as defined above, whereas physical and environmental ecotones should cause model 3 zonation of assemblages (Whittaker, 1967; Terborgh, 1971; Terborgh & Weske, 1975; Hofer *et al.*, 1999). Other factors, such as the environmental variables associated with climate, change only clinally with elevation, and there is no *a priori* reason why elevational zonation of communities should be identified in the absence of both species interactions and clearly defined ecotones (Kessler, 2000b). Nevertheless, a number of studies have now detected elevational boundaries of communities by employing statistical tests (Hofer *et al.*, 1999; Kessler, 2000b; Herzog *et al.*, 2005; Mena & Vázquez-Domínguez, 2005). In most cases, these boundaries can indeed be associated with well-defined ecotones, that is, with abruptly changing environmental conditions (Kessler, 2000b; Mena & Vázquez-Domínguez, 2005). It is unclear whether assemblages will organize themselves into distinct communities under gradually changing conditions, and the mechanism of such self-structuring among communities remains to be elucidated.

The present study analyses the distribution and abundance of birds from a forested tropical gradient in order to determine whether elevationally distinct communities are detectable. We

applied the chronological clustering method of Legendre *et al.* (1985), which provides unbiased estimates of the significance of boundaries. The data were collected by an intensive census of a single forest transect in the Udzungwa Mountains, Tanzania. Our null hypothesis is that gradual changes in floristic composition as well as in physical and climatic gradients are reflected in the avifauna, and that distinct lowland, submontane or montane bird communities will thus not be detectable. We discuss our findings in the light of current knowledge of community structure, range distribution, and species-richness patterns.

MATERIALS AND METHODS

An avifaunal census for the present study was carried out on the Mwanihana transect in the Udzungwa Mountains, Tanzania (Fig. 1). This site is part of the Eastern Arc Mountains, which stretch from the Taita Hills in south-east Kenya through to the Makambako Gap south-west of the Udzungwa Mountains in Tanzania (Lovett, 1990; Lovett & Wasser, 1993). The mountains are fault blocks of crystalline gneiss, shaped over tens of million of years, with the final uplift occurring 7 Ma (Griffiths, 1993). A consistent climatic regime has formed and has protected the unique forests covering these mountains (Lovett, 1993). The mountains are around 2200–2600 m a.s.l., with the major part of the gradient comprising Afromontane rain forest, and the lowest elevations encompassing Zanzibar-Inhambane transitional or lowland forest, as defined by Lovett (1990). The change in plant community composition is gradual, and boundaries between montane, submontane and lowland zones are generally applied by convention (Pócs, 1976; Lovett, 1993, 1996).

The trails leading up to the Mwanihana Peak (2010 m, at 7°49' S, 36°49' E) are found west of Mwanihana and Sonjo villages. Annual rainfall in this area is c. 2000–2500 mm, as measured at weather stations at the edges of the National Park (Tanzania Natural Resources Information Centre, unpublished data). From the base level of 300 m a.s.l., the entire gradient is covered by forest, with the exception of the upper 100 m a.s.l., which consist mainly of *Erica* heathland. The lowest reaches of the mountain (up to an elevation of c. 800 m a.s.l.) are covered in lowland forest intermingled with some *Miombo* woodland. At the uppermost elevations, the montane forest is interspersed with stands of bamboo, but the great majority of the gradient is uniform high-canopy Afromontane and Zanzibar-Inhambane rain forest (Lovett, 1993). The gradient has not been disturbed by human land use and is now part of the Udzungwa Mountains National Park. Our data are thus drawn exclusively from within the natural forest habitat.

All birds encountered within the forest were included in the data collection. Two complementary data sets were analysed. The first was based on a fully standardized 20-ha spot-mapping census (Bibby *et al.*, 2000) performed at nine elevations over 175-m intervals, namely 400, 575, 750, 925, 1100, 1275, 1450, 1625 and 1800 m a.s.l. The spot-mapping census is a method that aims to map accurately all individual

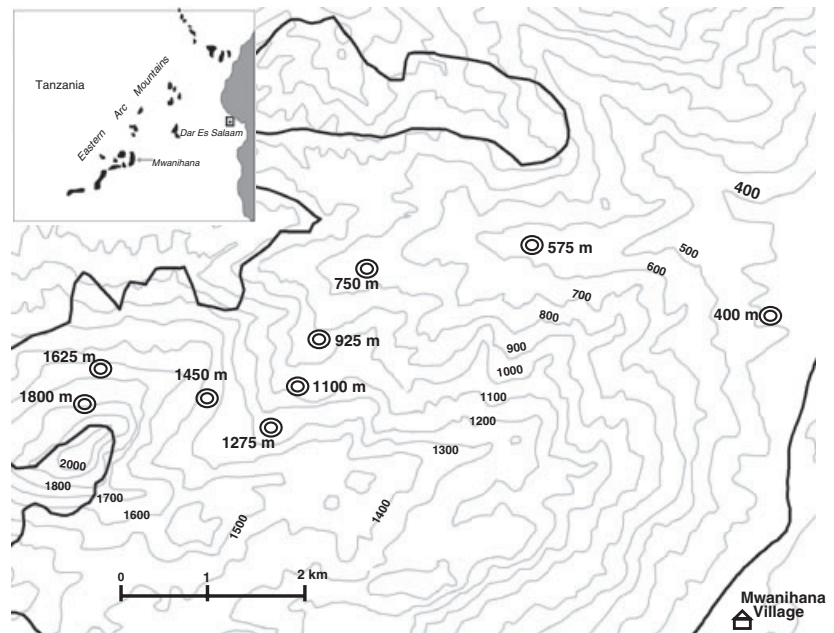


Figure 1 Map of the Mwanihana transect survey area with elevational contours for each 100 m. The position of each survey site is shown along with its elevation. Black contours represent forest boundaries. Insert: the position of the Mwanihana gradient within the Eastern Arc Mountains.

pairs of species within a plot, and at the same time yield area-related abundance data. Repeated observations of territorial behaviour, including singing, mating behaviour and parental behaviour, are used to construct the map. Spot-mapping was performed during October–December 2001, at the onset of the breeding season. Ten censuses were carried out on each plot, with the primary aim of recording territory-holding individuals. The second data set analysed combined all types of observations into presence records across 32 elevational intervals at a distance of 50 m, from 300 to 1850 m a.s.l. These data were obtained from survey efforts involving mistnetting, spot-mapping and general observations over the entire survey period from January to December 2001. It is a larger data set, but potentially biased owing to the variation among elevations within the respective survey efforts. Because spot-mapping data are included in the combined data set, the two data sets are not completely independent. However, only 17% of the data points (presence of species x at elevation y) in the combined data set overlap with the spot-mapping data set, and most of the species recorded at these spot-mapping data points were also recorded independently in general observations at the same site.

We examined the degree of zonation using the chronological clustering method described by Legendre *et al.* (1985), which is an agglomerative hierarchical clustering method that can be carried out using a range of similarity indices. This method has several distinct advantages over other clustering methods, in that: (1) it is a null-model approach that tests the significance of detected boundaries, (2) it tests all possible combinations of contiguous groupings of transect samples, whereas other methods only compare neighbouring samples, and (3) it is applicable to abundance data similarity as well as to presence–absence data. The chronological clustering method was developed for ecological studies on a temporal scale (succes-

sion), and uses the abundance of each species at a particular time as the computational unit. The method can easily be applied to biogeographical studies on a local spatial scale, where samples are taken at points on a spatial gradient (Galzin & Legendre, 1987). Accordingly, the method has been used on elevational herpetological data from Cameroon (Hofer *et al.*, 1999) as well as on botanical data from Mt Kilimanjaro (Hemp, 2002).

The R package software (Legendre, 2002) was used to perform the multidimensional and spatial analyses. The normalized data from individual samples (sites) constituted the clustered variable, and clustering was based on a matrix of site vs. site similarity. The method entailed the setting of two parameters, namely probability level (α) and *Connectedness* ($Co.$), the proportion of possible inter-cluster links used in calculation when fusing clusters (Legendre *et al.*, 1985). The value of α was set at 0.05, and we followed the recommended default of $Co. = 0.5$. Only boundaries detected at these levels will be discussed.

Steinhaus' coefficient (see Legendre, 2002) was used to detect boundaries in the spot-mapping data set, which includes information on the abundance of species. All data were log-transformed prior to analysis, in order to approach normality. Sørensen's index (see Legendre, 2002) was used on the presence–absence data from the complementary data set in order to see if the presence–absence data corroborate with the primary results. This data set contains gaps in the ranges where species were not recorded, either because they were not present at specific elevations, or because they were missed by the census procedure. On the extreme local scale of a single transect, unoccupied sections may exist, especially for species of low abundance. This problem was addressed by performing analyses both on the actually recorded point distributions and on interpolated distributions without gaps.

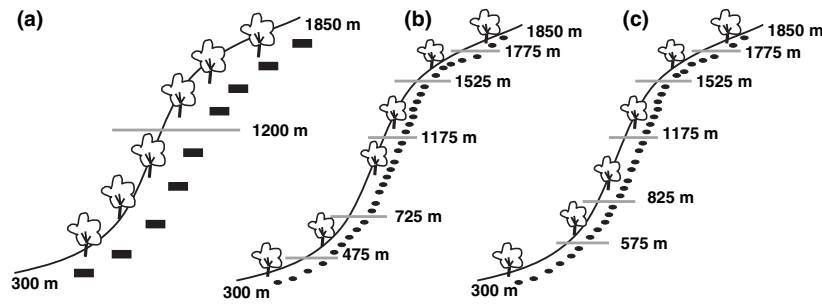


Figure 2 Results of the chronological clustering analysis of the two complementary data sets from the elevational gradient. Significant ($P < 0.05$) zonation boundaries are indicated by grey horizontal bars. (a) Results based on the analysis of abundance data from the spot-mapping data set from nine elevationally distributed spot-mapping areas (illustrated by black squares). (b) Results of the analysis of raw binary presence-absence data from the complementary data set from 32 stations (illustrated by black dots). These data are from all types of surveying, including the spot-mapping. (c) Presence-absence data as (b) but based on a data set with ranges interpolated between the lowest and highest elevational record.

RESULTS

Chronological clustering analysis of the abundance data based on spot-mapping identified a clearly defined boundary between stations 5 and 6, at c. 1200 m a.s.l., separating a lowland from a montane community (Fig. 2a). This boundary was also identified in the complementary data set based on all presence observations in the study area (Figs 2b,c). Owing to the greater statistical power of 32 data points, analyses of the complementary data set revealed additional boundaries. The results from the two versions of this analysis (using actual recorded and interpolated ranges, respectively) are nearly identical. Both identify the same number of boundaries (five) delimiting six zones, although the two lower boundaries are shifted 100 m upwards in the data set with interpolated, continuous ranges. A sensitivity analysis of the influence of the value of *Connectedness* ($Co.$) on the observed patterns of zonation is presented in Appendix S1 (see Supporting Information). A consistent, mid-elevational boundary for all data sets can be seen to be independent of the value of $Co.$

In Fig. 3, the interpolated elevational distributions of all species are shown schematically. Even though the lowland species community and the montane community are easily perceived at each end of this graph, it is clear that not all species are delimited by the clearly defined community boundary at 1200 m. The number of species found at each of 16 elevations is shown below the graph. On observing species distributions associated with the species-richness values, it appears that the very broad maximum of species richness at intermediate elevations is formed geometrically by two patterns of distributions. First, a number of species are found only at exactly these intermediate elevations. Second, and more pervasively, there are distinct lowland species that extend into higher elevations, and distinct highland species that extend into lower elevations, causing these two communities to have a broad overlap.

Figure 4 presents a pairwise similarity comparison, analysing trends in similarity between neighbouring elevations, for the presence-absence data set (32 stations along the elevational

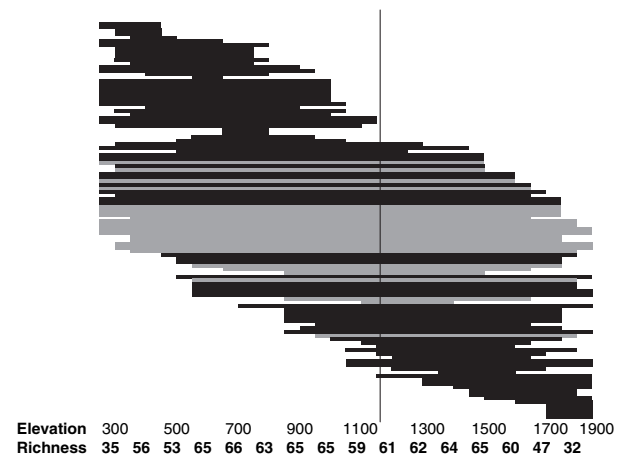


Figure 3 A graphical representation of the elevational distributions of all species. Each horizontal line represents the elevational range of one species, ordered by the elevation of the midpoint of the range. The species are categorized as lowland (black, top half), montane (black, lower half) or widespread (grey) according to Table 1. The vertical line shows the position of the main community boundary. Numbers below the graph show the number of species found at specific elevations (m) throughout the gradient.

gradient). This figure shows the number of species that have upper or lower limits at a given elevation, as well as (inverted) Sørensen similarity values. Both measures follow synchronous fluctuations, showing peaks where neighbouring sites are most dissimilar. Given the short elevational distance of 50 m between neighbouring stations, the numbers of shared species as well as the similarity values are generally high (between 0.7 and 1). Boundaries detected using the chronological clustering method (arrows, Fig. 4), appear to coincide with peaks in pairwise dissimilarity. A large peak in dissimilarity situated between the two lowest stations (at 325 m a.s.l.) was not detected by the chronological clustering analyses. This peak is, however, created entirely by lower distribution limits, that is, by species that are not found at the lowest elevation

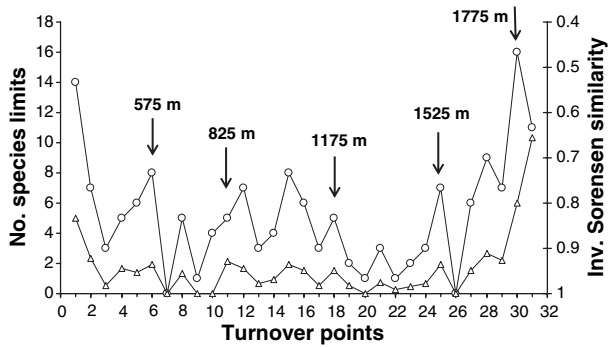


Figure 4 Pairwise similarity of the 32 intervals or stations along the elevational gradient at Mwanihana. The x-axis values represent shifts between neighbouring stations (i.e. the first data point is the similarity of stations 1 and 2). Similarity was calculated with the Sørensen index on the interpolated presence-absence data. The left y-axis (top plot, circles) shows the count of species upper and lower distributions limits, coincident with each turnover point. The right y-axis (lower plot, triangles) indicates the inverse pairwise Sørensen index similarity. This y-axis is reversed so that the two graphs fluctuate in parallel. Arrows show the positions of the five boundaries detected in the chronological clustering of the stations using interpolated ranges (Fig. 2c). This includes the main boundary identified following the chronological clustering of spot-mapping data (here: 1175 m a.s.l.).

(see Fig. 3), probably partly as a result of sampling deficiencies. Accordingly, a distinct community is not present at 300 m a.s.l.

Finally, Table 1 shows the complete list of species, with most species being tentatively allocated to either the lowland or the montane zone. There are several features worth noting from the list. First, the numbers of species found in the two major zones are similar (36 lowland and 40 montane species), suggesting two distinct and comparable communities. Second, half of the species in the entire survey (51 out of 109) were recorded *exclusively* in one of the two major zones, even though the non-breeding records contained in this combined data set would be expected to lead to greater overlap among zones.

DISCUSSION

Methodology

As a null-model tool, the chronological clustering method is a more suitable method with which to elucidate zonation patterns than traditional general clustering or ordination methods. However, this method requires a large number of elevationally distinct samples to maintain a high power of testing. With only nine samples, as was the case in our primary data set, it is difficult to identify significant boundaries at the outer extremes of the gradient, and 20 samples are needed before boundaries can be defined between the two outermost samples (Legendre *et al.*, 1985). To bypass the problem of power, and to reveal less-pronounced boundaries, Legendre

et al. (1985) recommended an increase in probability levels (α). This, however, increases the risk of type-I errors (finding too many significant boundaries), and the approach has subsequently been criticized (Burd *et al.*, 1990). The present study demonstrates that, even with a moderate number of samples, it is feasible to use abundance data to identify boundaries in seemingly homogenous habitats without compromising probability levels.

The use of abundance data, whenever these are available, has further advantages. One major factor that might obscure boundaries limiting bird communities is the mobility of the birds themselves. Most species can make forays into neighbouring habitats, and vagrant individuals can be found far from suitable habitats, or can be forced into habitats of low suitability by source sink dynamics (*sensu* Pulliam, 1988). An increased sampling effort within a survey will thus produce outliers in terms of more vagrant individuals. The application of abundance-sensitive measures overcomes this bias to a certain degree, as the impact of aberrant records is diminished.

To achieve a satisfactory outcome, data should: (1) preferably be collected from a minimum of 10 sites, and (2) contain abundance data for each species, as this greatly enhances the detection of boundaries. In the absence of abundance data, chronological clustering can be carried out on presence-absence data alone, although this requires larger samples. Other available measures of similarity performed on neighbouring sites, or on the community of samples (e.g. Connor & Simberloff, 1978), are not recommended, as autocorrelation invariably causes levels of similarity along the gradient to be higher than expected.

Patterns

We concur with the current perception that distinct elevational communities do exist, as has been demonstrated on various continents through the rigorous use of statistical testing (Hofer *et al.*, 1999; Kessler, 2000b; Mena & Vázquez-Domínguez, 2005). The transition between communities may be manifested as a gradual blending across a wide area, as is the case in the Mwanihana gradient, or as a more abrupt transition (Whittaker, 1967; Orłóci & Orłóci, 1990). A broader mid-elevational maximum of species turnover will coincide with the formation of a mid-elevational peak in species richness (Md. Nor, 2001; Herzog *et al.*, 2005; Mena & Vázquez-Domínguez, 2005), a finding that is in accordance with our own observations. The fundamental cause (i.e. when considering just the geography of the distributions) of a mid-elevational species-richness peak can either be the overlap of species ranges, or the fact that the mid-elevations have many unique species (Heaney, 2001). However, it is only in the former case that one may expect that distinct communities could be detected and identified. Accordingly, in our study on the Mwanihana gradient, we find that the broad peak in species richness is primarily associated with overlapping ranges of species belonging to one predominantly lowland and one predominantly highland community.

Table 1 The complete species list for the Mwanihana transect, tentatively assigned to elevational communities following the chronological clustering analyses. *Lowland* and *montane species* are those species for which 75% or more of records in the spot-mapping data set are found in the lowland zone (< 1200 m a.s.l.) and highland zone (> 1200 m a.s.l.), respectively (cf. Fig. 2a). Species that are exclusive to just one of the two major zones are highlighted in bold. *Widespread species* do not have 75% of records in one of the major zones. *Additional species* are species not recorded in the spot-mapping sampling, but recorded by other means and included in the fine-grain data set. The figures in parentheses after the species names indicate the number of pairs in all of the spot-mapping localities combined, as an index for how common the species is, followed by the zones of occurrence as identified and illustrated in Fig. 2b (1–3 are lowland, 4–6 are montane).

Lowland species	Widespread species	Montane species	Additional species
<i>Andropadus virens</i> (89 pairs, zones 1–5)	<i>Alethe fuelleborni</i> (39 pairs, zones 2–6)	<i>Accipiter tachiro</i> (3 pairs, zones 1–5)	<i>Accipiter minullus</i> (zone 1)
<i>Anthreptes collaris</i> (58, 1–4)	<i>Apalis melanocephala</i> (26, 2–5)	<i>Andropadus chlorigula</i> (25, 5–6)	<i>Anthreptes rubritorques</i> (2–3)
<i>Anthreptes neglectus</i> (6, 1–3)	<i>Batis mixta</i> (19, 2–5)	<i>Andropadus masukuensis</i> (22, 3–5)	<i>Apalis chariessa</i> (3–4)
<i>Apaloderma narina</i> (3, 1–3)	<i>Buteo oreophilus</i> (4, 3–6)	<i>Andropadus milanjensis</i> (33, 2–5)	<i>Apalis flavida</i> (1–3)
<i>Batis soror</i> (1, 1)	<i>Bycanistes brevis</i> (15, 1–6)	<i>Apalis chapini</i> (22, 3–6)	<i>Campethera abingoni</i> (2)
<i>Bias musicus</i> (1, 1–2)	<i>Coracina caesia</i> (42, 1–5)	<i>Apalis thoracica</i> (9, 3–6)	<i>Campethera caillauti</i> (1–3)
<i>Bycanistes buccinator</i> (1, 1–3)	<i>Indicator variegatus</i> (2, 2–4)	<i>Apaloderma vittatum</i> (19, 3–5)	<i>Chrysococcus cupreus</i> (4–5)
<i>Camaroptera brachyura</i> (28, 1–3)	<i>Mandingoa nitidula</i> (13, 1–4)	<i>Aplopelia larvata</i> (8, 2–6)	<i>Circaetus fasciolatus</i> (1–3)
<i>Campephaga flava</i> (1, 1–4)	<i>Nectarinia olivacea</i> (99, 1–5)	<i>Arcanator orostruthus</i> (2, 4–5)	<i>Merops oreobates</i> (2–3)
<i>Centropus superciliosus</i> (4, 1–6)	<i>Phyllastrephus flavostriatus</i> (23, 3–5)	<i>Artisornis metopias</i> (3, 4–6)	<i>Motacilla clara</i> (1–3)
<i>Cercotrichas quadrivirgata</i> (1, 1)	<i>Ploceus bicolor</i> (38, 1–5)	<i>Bradypterus cinnamomeus</i> (1, 5–6)	<i>Pitta angolensis</i> (1)
<i>Ceuthmochares aereus</i> (1, 1–3)	<i>Pogoniulus bilineatus</i> (17, 1–5)	<i>Bradypterus lopezi</i> (34, 2–6)	<i>Ploceus nicolli</i> (4–5)
<i>Chlorocicla flaviventris</i> (4, 1–3)	<i>Stactolaema olivacea</i> (42, 1–6)	<i>Cercococcyx montanus</i> (3, 3–5)	<i>Psalidoprocne pristoptera</i> (1–6)
<i>Cossypha natalensis</i> (39, 1–3)	<i>Stephanoaetus coronatus</i> (2, 1–6)	<i>Chrysococcyx klaas</i> (1, 1–4)	<i>Serinus burtoni</i> (4–6)
<i>Dendropicos fuscescens</i> (4, 1–4)	<i>Strix woodfordii</i> (4, 1–5)	<i>Columba arquatrix</i> (3, 4–6)	<i>Telecanthura ussheri</i> (1–4)
<i>Dicrurus ludwigii</i> (41, 1–5)	<i>Swynnertonia swynnertonii</i> (5, 3–4)	<i>Columba delegorguei</i> (29, 2–6)	
<i>Dryoscopus cubla</i> (11, 1–3)	<i>Tauraco livingstonii</i> (23, 1–6)	<i>Cossypha anomala</i> (4, 5–6)	
<i>Francolinus squamatus</i> (6, 2–3)	<i>Terpsiphone viridis</i> (11, 1–5)	<i>Cryptospiza reichenovii</i> (86, 3–6)	
<i>Guttera pucherani</i> (15, 1–5)		<i>Elminia albonotata</i> (15, 3–5)	
<i>Hypargos niveoguttatus</i> (2, 1–3)		<i>Laniarius fuelleborni</i> (5, 4–6)	
<i>Ispidina picta</i> (9, 1–3)		<i>Malaconotus nigrifrons</i> (7, 2–5)	
<i>Lamprotornis corruscus</i> (2, 1)		<i>Mesopicos griseocephalus</i> (3, 4–5)	
<i>Laniarius aethiopicus</i> (2, 1–3)		<i>Modulatrix stictigula</i> (4, 5–6)	
<i>Macrosphenus kretschmeri</i> (6, 1–3)		<i>Muscicapa adusta</i> (1, 1–4)	
<i>Muscicapa caerulescens</i> (1, 1)		<i>Nectarinia moreaui</i> (39, 4–6)	
<i>Myioparus plumbeus</i> (1, 1–3)		<i>Nectarinia rufipennis</i> (7, 4–5)	
<i>Nicator gularis</i> (5, 1–3)		<i>Onychognathus morio</i> (7, 5–6)	
<i>Oriolus chlorocephalus</i> (32, 1–5)		<i>Onychognathus walleri</i> (21, 2–6)	
<i>Phyllastrephus cerviniventris</i> (1, 2–3)		<i>Phoeniculus purpureus</i> (2, 1–5)	
<i>Phyllastrephus fischeri</i> (8, 1–3)		<i>Phyllastrephus cabanisi</i> (9, 3–5)	
<i>Prionops retzii</i> (3, 1–3)		<i>Phylloscopus ruficapillus</i> (25, 3–6)	
<i>Pycnonotus barbatus</i> (11, 1–6)		<i>Poeoptera kenrickii</i> (4, 3–5)	
<i>Stactolaema leucotis</i> (4, 1–3)		<i>Pogoniulus leucomystax</i> (4, 4–6)	
<i>Tockus alboterminatus</i> (5, 1–5)		<i>Pogonocichla stellata</i> (42, 2–6)	
<i>Trochocercus cyanomelas</i> (15, 1–3)		<i>Pseudoalcippe abyssinica</i> (1, 5–6)	
<i>Turtur tympanistris</i> (37, 1–5)		<i>Sheppardia sharpei</i> (41, 3–5)	
		<i>Smithornis capensis</i> (27, 1–5)	
		<i>Turdus olivaceus</i> (6, 3–6)	
		<i>Zoothera gurneyi</i> (5, 3–5)	
		<i>Zosterops senegalensis</i> (26, 2–6)	

In accordance with our findings, Mena & Vázquez-Domínguez (2005), in a meta-analysis of mammalian studies, found that intermediate elevations are often where species turnover is highest, across a wide spectrum of ecologically different gradients. This new knowledge correlates with the mid-elevational peak in species richness now being recognized as the most predominant empirical pattern (Rahbek, 2005). Theoretically, a boundary separating two distinct communities could also exist without a peak in species richness (model 1, Whittaker, 1967). This could be the case if, for example, a very abrupt environmental change was the primary determinant of the placement of boundaries (Beals, 1969; Kessler, 2000b; Mena & Vázquez-Domínguez, 2005). For instance, in the Sierra Madre del Sur in Mexico, Navarro (1992) found one out of two ecotones to be situated at the upper limit of coffee cultivation. On the other hand, source-sink dynamics (i.e. spillover of individuals into neighbouring habitat types and elevations, *sensu* Pulliam, 1988) will tend to eliminate any sharp boundaries, leading to an increase in species richness around the zones of maximum turnover (Rahbek, 1997; Grytnes, 2003). Therefore, the identification of a rigid structuring resembling Whittaker's model 1 (i.e. sharply defined, mutually exclusive communities) in empirical data appears to be unlikely (Auerbach & Shmida, 1993; Grytnes, 2003). It is more likely that a situation similar to Whittaker's model 3 (i.e. distinct communities with broad zones overlap) will be identified. Accordingly, it is surprising that Kessler (2000b) did not find that statistically detected discontinuities on a number of Andean gradients were associated with species-richness peaks. Although assemblage boundaries coincided with physical (i.e. abrupt changes in slope and terrain) and geological (soil type) phenomena, as well as with changes from deciduous to evergreen to non-forest habitats, peaks in species richness did not appear to correlate with these phenomena (Kessler, 2000b). Other studies have failed to find an association between species-richness peaks and apparent ecotones (Odland & Birks, 1999; Grytnes, 2003; McCain, 2004), and the significance of the source-sink effect for richness patterns is still a matter of contention. Finally, zones with the highest turnover of species are not necessarily associated with the highest species richness, as the gradual elimination of species with increasing elevation is in itself a form of turnover (Rahbek, 1997).

Mechanisms

In our study site, no abrupt discontinuities of a physical, geological, or vegetational nature are apparent in the central part of the gradient, although it is possible that a vegetational transition zone was simply not registered. Nonetheless, two different, partly exclusive, avian assemblages seem to have developed over time through individual and community adaptations. In an afro-tropical forest in Cameroon, Hofer *et al.* (1999) also detected a broad turnover zone separating a lowland and highland herpetofauna, but with many more species in the community at lower elevations,

such that the boundary was not associated with a mid-elevational richness peak. We have identified another zonation structure, in which the overlap of distinct communities within a homogeneous habitat is associated with the tendency for species richness to peak at intermediate elevations.

At this point it is evident that zonation patterns conforming to both Whittaker's model 1 (exclusive) and model 3 (overlapping) can be demonstrated using empirical data. The paradigm that species interactions cause model 1 zonation whereas ecotones cause model 3 zonation is, however, not strongly supported in the literature. Specifically, ecotones appear to delimit both overlapping and non-overlapping communities, whereas the mechanism of interspecific interaction has never been rigorously analysed. Terborgh (1985) compared the locations of bird distribution limits with the locations of ecotones on a number of mountains in the Andes. He argued that competition was responsible for two-thirds of the bird species range limits, whereas predefined habitat ecotones were responsible for only one-sixth of the range limits (Terborgh, 1985). In contrast, Hofer *et al.* (1999), in their randomization analysis of reptiles and amphibians in Cameroon, found that hypothesized congeneric competition rarely caused altitudinal segregations, and Cadena & Loiselle (2007) showed that variation in elevational range limits of finches was more related to autecology and geographic variation in the environment than to the presence or absence of competitors. In addition, Hofer *et al.* (2000) found that predefined vegetational zones were poor predictors of reptile and amphibian distributions, although there were certain detectable, inherent discontinuities of communities. Most species responded primarily to gradual changes in habitat (Hofer *et al.*, 2000). On the other hand, Patterson *et al.* (1998), in their study of the birds and mammals of the Andes, found that species range limits were indeed clustered near the ecotones that Terborgh (1971) had defined, and that particular groups of species occupy the zones between ecotones.

The data in the present study do not allow for the assessment of competition pressure; no studies have definitively demonstrated the influence of competition on the elevational distributions of tropical organisms, although speculations abound (see Romdal, 2001). The basis for the self-organization of the two communities on the Mwanihana gradient is therefore unclear, but is very likely to relate to adaptations to climatically changing microclimatic variables (Hofer *et al.*, 1999), to emerging positive interactions among species that share the same elevations, and to negative interactions among species at different elevations (Terborgh & Weske, 1975; Romdal, 2001). Another possibility is that montane and lowland communities may in part have evolved from elevational forest refugia. In the Pleistocene the climate of East Africa was cyclically drier, and forest cover on mountain ranges was periodically restricted to higher elevations, with other forest types existing on river floodplains (Fjeldså & Lovett, 1997), permitting the evolution of distinct lowland and

montane communities. A similar reduction in forest habitat was also evident during much earlier periods, such as the Eocene (Jacobs & Herendeen, 2004), so a tendency towards lowland and montane forest taxa specialization may be an underlying historical characteristic of the Eastern Arc assemblage.

The variation among zonation patterns on gradients from different continents and climate zones, as well as for different organism groups is enormous (Roy *et al.*, 1997; Patterson *et al.*, 1998; Mena & Vázquez-Domínguez, 2005). We are thus far from a general understanding of the interplay of patterns of species turnover and patterns of species richness. The increased overlap of species ranges (and therefore the higher number of species) reported at mid-elevations is a key characteristic of geometric null models (the mid-domain effect, Colwell & Lees, 2000; Cardelus *et al.*, 2006), but null models, by definition, do not incorporate the effect of structuring of communities. In fact, the prediction of current geometric null models is for a higher turnover among species near the extremes of the elevational domain, not in the centre (Mena & Vázquez-Domínguez, 2005). Paradoxically, even though the mid-domain effect can explain why more species are found at mid-elevations, it fails to account for the presence of mid-elevation community boundaries in cases where they occur (Herzog *et al.*, 2005). For the specific objective of investigating the patterns and causes of zonation, chronological clustering or similar rigorous gradient analysis tools are recommended. Further research should aim to discriminate causes from effects in species distribution patterns, species turnover patterns, peaks of species richness and environmental factors.

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REFERENCES

Auerbach, M. & Shmida, A. (1993) Vegetation change along an altitudinal gradient on Mt Hermon, Israel – no evidence for discrete communities. *Journal of Ecology*, **81**, 25–33.

- Beals, E.W. (1969) Vegetational change along altitudinal gradients. *Science*, **165**, 981–985.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. (2000) *Bird census techniques*. Academic Press, London.
- Burd, B.J., Nemeč, A. & Brinkhurst, R.O. (1990) The development and application of analytical methods in benthic marine infaunal studies. *Advances in Marine Biology*, **26**, 169–247.
- Cadena, C.D. & Loiselle, B.A. (2007) Limits to elevational distributions in two species of Emberizine finches: disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. *Ecography*, **30**, 491–504.
- Cardelus, C.L., Colwell, R.K. & Watkins, J.E. (2006) Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology*, **66**, 1247–1260.
- Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, **15**, 70–76.
- Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: What have we learned so far? *The American Naturalist*, **163**, E1–E23.
- Connor, E.F. & Simberloff, D. (1978) Species number and compositional similarity of the Galapagos flora and avifauna. *Ecological Monographs*, **48**, 219–248.
- Cornelius, J.M. & Reynolds, J.F. (1991) On determining the statistical significance of discontinuities within ordered ecological data. *Ecology*, **72**, 2057–2070.
- Fjeldså, J. & Lovett, J.C. (1997) Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centers. *Biodiversity and Conservation*, **6**, 325–347.
- Galzin, R. & Legendre, P. (1987) The fish communities of a coral reef transect. *Pacific Science*, **41**, 158–165.
- Griffiths, C.J. (1993) The geological evolution of East Africa. *Biogeography and ecology of Eastern Africa* (ed. by J.C. Lovett and S.K. Wasser), pp. 9–22. Cambridge University Press, Cambridge.
- Grytnes, J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291–300.
- Heaney, L.R. (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, **10**, 15–39.
- Hemp, A. (2002) Ecology of the pteridophytes on the southern slopes of Mt Kilimanjaro. *Plant Ecology*, **159**, 211–239.
- Herzog, S.K., Kessler, M. & Bach, K. (2005) The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography*, **28**, 209–222.
- Hofer, U., Bersier, L. & Borcard, D. (1999) Spatial organization of a herpetofauna on an elevational gradient revealed by null-model tests. *Ecology*, **80**, 976–988.
- Hofer, U., Bersier, L. & Borcard, D. (2000) Ecotones and gradient as determinants of herpetofaunal community

- structure in the primary forest of Mount Kupe, Cameroon. *Journal of Tropical Ecology*, **16**, 517–533.
- Jacobs, B.F. & Herendeen, P.S. (2004) Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **213**, 115–123.
- Kessler, M. (2000a) Upslope-directed mass effect in palms along an Andean elevational gradient: a cause for high diversity at mid-elevations? *Biotropica*, **32**, 756–759.
- Kessler, M. (2000b) Altitudinal zonation of Andean cryptogam communities. *Journal of Biogeography*, **27**, 275–282.
- Legendre, P. (2002) *The R Package for multidimensional and spatial analysis*. [WWW document]. Available at: <http://www.bio.umontreal.ca/Casgrain/en/labo/R/index.html>; last accessed 9 November 2008.
- Legendre, P., Dallot, L. & Legendre, L. (1985) Succession of species within a community: chronological clustering, with applications to marine and freshwater zooplankton. *The American Naturalist*, **125**, 257–288.
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.
- Lovett, J.C. (1990) Classification and status of the moist forests of Tanzania. *Mitteilungen Institut Allgemeiner Botanik*, **23a**, 287–300.
- Lovett, J.C. (1993) Eastern Arc moist forest flora. *Biogeography and ecology of the rain forests of Eastern Africa* (ed. by J.C. Lovett and S.K. Wasser), pp. 33–55. Cambridge University Press, Cambridge.
- Lovett, J.C. (1996) Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc mountains of Tanzania. *Journal of Tropical Ecology*, **12**, 629–650.
- Lovett, J.C. & Wasser, S.K. (eds) (1993) *Biogeography and ecology of Eastern Africa*. Cambridge University Press, Cambridge.
- McCain, C.M. (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, **31**, 19–31.
- Md. Nor, S. (2001) Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography*, **10**, 41–62.
- Mena, J.L. & Vázquez-Domínguez, E. (2005) Species turnover on elevational gradients in small rodents. *Global Ecology and Biogeography*, **14**, 539–547.
- Navarro, A.G. (1992) Altitudinal distribution of birds in the Sierra Madre del Sur, Guerrero, Mexico. *Condor*, **94**, 29–39.
- Odland, A. & Birks, H.J.B. (1999) The altitudinal gradient of vascular plant richness in Aurland Western Norway. *Ecography*, **22**, 548–566.
- Orlói, L. & Orlói, M. (1990) Edge detection in vegetation: Jornada revisited. *Journal of Vegetation Science*, **1**, 311–324.
- Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W. & Pacheco, V. (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of south-eastern Peru. *Journal of Biogeography*, **25**, 593–607.
- Pendry, C.A. & Proctor, J. (1997) Altitudinal zonation of rain forest on Bukit Belalong, Brunei: soils, forest structure and floristics. *Journal of Tropical Ecology*, **13**, 221–241.
- Pócs, T. (1976) Bioclimatic studies in the Uluguru Mountains (Tanzania, East Africa). II. Correlations between orography, climate and vegetation. *Acta Botanica Academica Scientiarum Hungariae*, **22**, 163–183.
- Pulliam, H.R. (1988) Sources, sinks and population regulation. *The American Naturalist*, **132**, 652–661.
- Rahbek, C. (1997) The relationship among area, elevation, and regional species richness in neotropical birds. *The American Naturalist*, **149**, 875–902.
- Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224–239.
- Romdal, T.S. (2001) Altitudinal distribution and abundance patterns of bird species in the Eastern Arc Mountains, Tanzania. *Scopus*, **21**, 35–54.
- Roy, M.S., Cardoso da Silva, J.M., Arctander, P., Garcia-Moreno, J. & Fjeldså, J. (1997) The speciation of South American and African birds in montane regions. *Avian molecular evolution and systematics* (ed. by D.P. Mindell), pp. 325–343. Academic Press, San Diego.
- Terborgh, J. (1971) Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology*, **52**, 23–40.
- Terborgh, J. (1977) Bird species diversity on an Andean elevational gradient. *Ecology*, **58**, 1007–1019.
- Terborgh, J. (1985) The role of ecotones in the distribution of Andean birds. *Ecology*, **66**, 1237–1246.
- Terborgh, J. & Weske, J.S. (1975) The role of competition in the distribution of Andean birds. *Ecology*, **56**, 562–576.
- Tuomisto, H., Ruokolainen, K., Aguilar, M. & Sarmiento, A. (2003) Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology*, **91**, 743–756.
- Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biological Review*, **42**, 207–264.

SUPPORTING INFORMATION

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Appendix S1 Sensitivity analysis of the parameter *Connect-edness* (*Co.*) in the chronological clustering method.

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