



Unusual abundance–range size relationship in an Afrotropical bird community: the effect of geographical isolation?

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ABSTRACT

Aim To show that the frequently reported positive trend in the abundance–range–size relationship does not hold true within a montane bird community of Afrotropical highlands; to test possible explanations of the extraordinary shape of this relationship; and to discuss the influence of island effects on patterns of bird abundance in the Cameroon Mountains.

Location Bamenda Highlands, Cameroon, Western Africa.

Methods We censused birds during the breeding season in November and December 2003 using a point-count method and mapped habitat structure at these census points. Local habitat requirements of each species detected by point counts were quantified using canonical correspondence analysis, and the size of geographical ranges of species was measured from their distribution maps for sub-Saharan Africa. We tested differences in abundance, niche breadth and niche position between three species groups: endemic bird species of the Cameroon Mountains, non-endemic Afrotropical species, and widespread species.

Results We detected neither a positive nor negative abundance–range–size relationship in the bird community studied. This pattern was caused by the similar abundance of widespread, endemic and non-endemic montane bird species. Moreover, endemic and non-endemic montane species had broader local niches than widespread species. The widespread species also used more atypical habitats, as indicated by the slightly larger values of their niche positions.

Main conclusions The relationship detected between abundance and range size does not correspond with that inferred from contemporary macroecological theory. We suggest that island effects are responsible for the observed pattern. Relatively high abundances of montane species are probably caused by their adaptation to local environmental conditions, which was enabled by climatic stability and the isolation of montane forest in the Cameroon Mountains. Such a unique environment provides a less suitable habitat for widespread species. Montane species, which are abundant at present, may also have had large ranges in glacial periods, but their post-glacial distribution may have become restricted after the retreat of the montane forest. On the basis of comparison of our results with studies describing the abundance structure of bird communities in other montane areas in the Afrotropics, we suggest that the detected patterns may be universal throughout Afrotropical forests.

Keywords

Bamenda Highlands, bird endemism, Cameroon Mountains, geographical range size, macroecology, montane forest, niche breadth, niche position, rarity.

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INTRODUCTION

The positive abundance–range-size relationship (hereafter ARSR) is one of the best documented macroecological patterns, reported for various taxa and at various spatial scales (for review see Gaston & Blackburn, 2000). Despite the generality of the pattern, there is still considerable disagreement about the mechanism that generates it. Gaston *et al.* (1997) reviewed eight hypotheses accounting for the ARSR. Some of these, such as sampling artefacts and phylogenetic non-independence of data, are treated as unreliable explanations (but cf. Symonds & Johnson, 2006). From biologically relevant hypotheses, the most frequently considered is the ‘niche-breadth’ hypothesis (Brown, 1984), which states that species exploiting the widest array of resources are locally abundant, and have large ranges at the same time. Gregory & Gaston (2000) stressed resource availability instead of niche breadth in their ‘niche-position’ hypothesis. They found that species specialized to marginal resources have the lowest abundances and the smallest range sizes, whereas widespread and locally abundant species are adapted to widely distributed habitats. Other hypotheses are based on population processes (Holt *et al.*, 2002). For instance, species with locally abundant populations have many floating individuals that colonize new suitable habitat patches and thus prevent range compression (the ‘metapopulation dynamics’ explanation; Hanski, 1982, 1999). However, particular hypotheses are probably not mutually exclusive. The strength of the impact of each factor can vary in different situations (Gaston & Blackburn, 2000) and several mechanisms may operate in concert (Heino, 2005).

Although the positive ARSR is a general pattern in species assemblages throughout the world, some exceptions exist. Gaston & Lawton (1990) found that the relationship becomes non-significant or even negative when the habitat in which the abundances are measured differs markedly from the spectrum of common habitats in the respective geographical region. Species specialized to unusual habitats have high abundances in localities where they occur but are unable to disperse to other areas. However, habitat composition is not the only factor affecting local species abundances. Brown (1995) suggested deviations from the positive trend of ARSR in island communities. High abundance of island endemics is caused by two factors: (i) islands are species-poor, interspecific competition is therefore less intensive and individual species can exploit a greater amount of resources (MacArthur *et al.*, 1972); (ii) island communities are isolated and the environment is often stable, so species have a long time for adaptation to local environmental conditions (Thiollay, 1997). Such adaptation is enabled by the restricted gene pool of the island population, whereas permanent gene flow prevents such a process on the mainland. On the other hand, widely distributed species that have recently colonized an island may have low abundances because they are exposed to an unknown environment already occupied by well adapted local species (Jones *et al.*, 2001).

The unique environment and geographical isolation of high-altitude areas in the tropics generate several island patterns, such as low species richness (Rahbek, 1995); a high proportion of endemic species (Fjeldså & Lovett, 1997a); and high local abundances of endemic species (Manne *et al.*, 1999). However, Kattan (1992) found that bird species with the smallest ranges also had low abundances in the Columbian Cordillera. Thus, further investigation of abundance structure in montane bird communities in the tropics is needed to provide relevant data for the exploration of mechanisms leading to the origin of these patterns.

In the Cameroon Mountains, the montane forest represents an island in a sea of lowland rain forest and savanna (Mayaux *et al.*, 2004). It is assumed that it underwent large changes in its distribution during the Quaternary (Elenga *et al.*, 2000). It was distributed in lower altitudes in glacial periods and was probably merged with the lowland forest, forming an environment with continent-wide distribution. Conversely, in periods of global climatic optima, the montane forest retreated to higher altitudes and became fragmented. For instance, recent distribution of the upper montane forest in the Cameroon Mountains has a lower elevation limit at altitudes of about 1600 m a.s.l. (Thomas, 1986) and the nearest larger blocks of similar habitat occur in Eastern Africa. Thanks to this isolation and long-term climatic stability (Fjeldså & Lovett, 1997b), the Cameroon Mountains host specific bird communities with a high proportion of endemic species (Stuart, 1986). West African forests are recognized as a hotspot of bird endemism of regional (Stattersfield *et al.*, 1998; De Klerk *et al.*, 2004) and global importance (Orme *et al.*, 2005).

Although the Cameroon Mountains seem to be an ideal model for the exploration of island effects on abundances of montane bird species, so far the local community structure has been poorly studied. To our knowledge, there has been no previous study attempting to examine the influence of endemism on the shape of ARSR in an afro-tropical montane environment. The aims of our study are thus: (i) to assess precisely the abundances and habitat requirements of bird species in a local bird community in the Cameroon Mountains; and (ii) to discuss the shape of ARSR in this Afromontane bird community in view of island effects and habitat specificity.

METHODS

Study area

The study was performed in the area named My Ogade in the Bamenda Highlands, North-West Province, Cameroon (geographical position: 06°05′26″ N, 10°18′09″ E; 2200 m a.s.l.). The study site was selected so that all major habitat types of the Cameroon Mountains were present in their natural proportions. The area covered about 1 km² and comprised several habitats including upper montane forest (according to Cheek *et al.*, 2000), *Gnidia glauca* woodlands, montane grasslands dominated by *Sporobolus africanus*, species-rich shrub vegetation, intensive pastures dominated by *Pennisetum*

clandestinum, species-rich extensive pastures, abandoned fields with ruderal plant species, forest clearings dominated by *Peridium aquilinum*, and densely vegetated corridors alongside streams. The montane forest was represented by two large patches (c. 20 ha) and several small fragments (0.1–1 ha).

Bird sampling

The bird census was carried out using a point-count method (Bibby *et al.*, 2000), which is recommended for areas with dense vegetation cover and high species richness (Gregory *et al.*, 2003). To maximize sampling efficiency, we established two perpendicular transects where we located 50 census points at 100 m distances. The first transect contained 20 points, the second 30 points. Transects were as straight as possible and covered all main habitat types within the study area.

We performed bird censuses from 24 November to 14 December 2003. The dry season begins at that time in the Bamenda Highlands (Tye, 1986) and most bird species start breeding (Serle, 1981; Tye, 1991). For 3 weeks before the census started, we trained intensively in the determination of all bird species using our own tape recordings. We had also spent 2 months observing birds in the Cameroon Mountains in 2001. We conducted three visits to each census point, recording all birds (both visually and acoustically) within a 50-m radius for 10 min on each visit.

For more precise estimates of species densities, distance sampling is frequently used (Bibby *et al.*, 2000). At our study plot, we recognized that the construction of detectability curves (*sensu* Buckland *et al.*, 1993) would be unreliable because of low count numbers of most species. Therefore we decided to use a narrow fixed radius (50 m) in which the detectability for all species was almost the same. We are convinced that abundance estimates for particular species are adequate for interspecific comparisons.

We performed all visits during morning hours (between 6:30 and 10:00), changing the order of points visited to factor out the effect of daytime. The maximum counts recorded from all visits were taken as the species' abundance at a particular point. The abundance of a species in the study plot was calculated as the sum of point abundances.

Range sizes were calculated from the distributional maps in Sinclair & Ryan (2003) using IMAGE TOOL Ver. 3.00 software (Department of Dental Diagnostic Science at the University of Texas, Health Science Center, San Antonio, TX, USA, 1995–2002). We sorted all species into three categories: (i) endemics of the Cameroon Mountains; (ii) montane species non-endemic to the Cameroon Mountains; and (iii) species widespread throughout Africa occurring in both lowlands and highlands. Species with ranges in elevations mostly above 1200 m a.s.l. were considered to be montane species (*sensu* Graham *et al.*, 2005).

Vegetation sampling

We estimated the relative coverage of particular vegetation layers in a 50-m radius around each census point. We

distinguished five vegetation layers: up to 1 m, 1–3 m, 3–5 m, 5–10 m and > 10 m above the ground. We also estimated the degree of continuity of shrub and forest, respectively, on a scale from 1 (solitary trees or bushes) to 5 (one continuous block).

Data analyses

We analysed the shape of ARSR by plotting the species' local abundance against range size on a log–log scale, and tested the significance of this relationship by the Pearson correlation coefficient. Although the local abundance does not reliably estimate the average abundance throughout the whole species range, it is applicable in studies dealing with mechanisms generating ARSR at local scale (Gaston & Lawton, 1990).

We used one-way ANOVA to assess differences in the average abundance between the three species groups (endemics, non-endemic montane species and widespread species). For data analyses, we excluded eight species of aerial feeders and raptors because of the high probability of counting the same individuals at more than one census point. Data on abundance were log-transformed to improve normality.

For a more accurate illustration of the influence of particular species on the shape of ARSR, we constructed a new variable called 'abundance–range–size ranking difference', which was calculated as follows. We ordered species according to abundance and range size, respectively. If the positive ARSR is assumed, the abundance rank for a particular species will correspond to its range–size rank. We therefore calculated the differences between these two rankings for each species. The absolute value of the difference shows the degree of deviation from positive ARSR, while its sign indicates whether the species abundance is higher or lower than expected by range size.

The local niche breadth of each species can be viewed as the tolerance of the species to particular habitat factors sampled at the study plot (Gregory & Gaston, 2000). We used canonical correspondence analysis (CCA) to relate the data on bird abundance to vegetation variables. CCA is a multivariate direct–gradient analysis technique, which is able to detect the patterns of variation in bird community composition that can be explained by the set of environmental variables. CCA ordines samples (census points) and variables (bird species and habitats) along axes such that the differences among species and samples, respectively, are maximized. Each ordination axis represents an environmental gradient along which the centroids of individual variables and samples are distributed so as to maximize differences between them (Storch *et al.*, 2002). CCA is based on the assumption that species distributions are unimodal along environmental gradients. The species score is proportional to the mean of sample scores weighted by abundance of respective species, and indicates the centre of distribution of the species. The width of the distribution along axes, as quantified by the standard deviation, can be used as a measure of niche breadth (ter Braak & Šmilauer, 2002). Niche position was assessed as the Euclidean distance of species scores from the score of the

whole community, which was calculated as the arithmetic mean of coordinates of the species scores. A high value of niche position indicates that a species uses more atypical habitats compared with the community as a whole (Gregory & Gaston, 2000). CCA was performed in CANOCO for Windows (ter Braak & Šmilauer, 2002). The CCA-based niche breadth cannot be calculated for species detected at less than two census points, and thus we excluded 14 species from the analyses dealing with niche variables. Both local niche breadth and local niche position express only local habitat requirements of a particular species in the study area, and cannot be viewed as descriptors for total species tolerance to all environmental conditions throughout their geographical ranges.

RESULTS

In total, we recorded 71 bird species within the study area (Table 1). We detected 11 endemics of the Cameroon Mountains, 17 non-endemic afro-tropical montane species, and 43 widespread species not strictly bound to montane environments. In this assemblage, we found neither a positive nor negative trend in ARSR (Pearson $R = 0.07$, $n = 63$, $P = 0.59$). However, the graphical visualization of the species in the abundance–range size space revealed a striking clustering pattern according to range sizes of endemic, non-endemic montane and widespread species (Fig. 1). The average abundances among these species groups were similar (ANOVA, d.f. = 2, 60; $F = 1.18$, $P = 0.31$). However, about 60% of the Cameroon Mountains endemics and non-endemic montane species have relatively high abundances (Fig. 1).

The analysis of differences among particular species groups in the abundance–range-size ranking difference (see Methods) revealed that the endemic species and non-endemic montane species have positive differences between rankings, whereas widespread species have negative ones (Kruskal–Wallis test, d.f. = 2, 60; $H = 29.76$, $P < 0.001$; Fig. 2), indicating higher abundances relative to range sizes in endemics and non-endemic montane species, and the opposite in widespread species.

We found significant differences in local niche breadth among particular species groups (niche breadth, ANOVA, d.f. = 2, 46; $F = 6.23$, $P < 0.01$). The niche breadth of non-endemic montane species and endemic species is wider than the niche breadth of widespread species (Fig. 3a). The widespread species have slightly larger values of local niche position (Fig. 3b), although this difference is not significant (ANOVA, d.f. = 2, 46; $F = 2.53$, $P = 0.09$).

DISCUSSION

We found no significant relationship between local abundance and range size within a montane bird community in the Bamenda Highlands. Our results demonstrate that: (i) most of the montane species (including the Cameroon Mountains endemics) have relatively high local abundances; and (ii) many widespread species are less abundant. Our findings are in

conflict with one of the general macroecological rules, which states that widespread species will be more abundant than species with small ranges (Brown, 1995; Gaston & Blackburn, 2000).

Gaston *et al.* (1997) suggest poor data as one explanation for the absence of significance in ARSR. We are convinced this is not the case in our study. Insufficiencies in the data could be caused by inadequate timing of censuses with respect to breeding season, which lasts all year round in the tropical rain forest (Stutchbury & Morton, 2001). However, unusually heavy rainfall and high humidity cause a rapid decline of temperature with altitude, which prevents almost all bird species from breeding during the wet season in the Cameroon Mountains (Serle, 1981; Tye, 1991). Thus, although our bird censuses were restricted to the dry season, we registered almost all birds during their breeding period. We recorded all species confined to the upper montane forest environment (in comparison with Stuart & Jensen, 1986; Fotso, 2001) except *Apaloderma vittatum* and *Aplopelia larvata*. Other montane species reported by Fotso (2001) from the Mount Oku area (*Kakamega poliothorax*, *Laniarius poensis*, *Phyllastreptus poensis* and *Malaconotus gladiator*) are distributed mostly at lower altitudes, up to 2200 m a.s.l. (Stuart & Jensen, 1986).

We argue that the detected shape of ARSR has a relevant biological justification. The main proximate causes are: (i) relative high abundances of endemic and non-endemic montane species; and (ii) relative low abundances of widespread species. Although the data on precisely assessed species abundances in Afro-montane bird communities are rather scarce, it seems that this pattern is not unusual within the afro-tropical region. Sekercioğlu & Riley (2005) found that endemic species are among the most abundant in the Kumbira Forest in the Angola Escarpment. Similarly, endemic and non-endemic montane species have a higher number of counts than widespread species on the Namuli Massif in northern Mozambique (Ryan *et al.*, 1999). Endemic species have high detection rates in montane forest environment in the Albertine Rift, and form a substantial part of bird communities in elevations 2100–2600 m a.s.l. (Owiunji *et al.*, 2005). Fjeldså (1999) and Fjeldså & Rabøl (1995) found that the endemics of the Eastern Arc Mountains are abundant in the mature montane forest. These studies illustrate that endemic and non-endemic montane species also have high abundances in other African mountains. This suggests that the ARSR observed in our study area is of wider relevance.

What mechanism triggers high local abundances of montane species and low abundances of widespread species? Gaston & Lawton (1990) provide detailed analysis of the influence of habitat structure on the shape of ARSR. They show that the positive ARSR becomes non-significant and even negative when the abundances of species are estimated in a habitat that differs markedly from the spectrum of habitats in the region where the species ranges are measured. Gaston & Lawton (1990) argue that widespread species have low abundance in unusual habitats, whereas species specialized to these habitats cannot expand their ranges. Our results confirm their finding,

Table 1 Characteristics of species registered during point counts in the My Ogade area, Bamenda Highlands, Cameroon

Species	Status	Abundance (no. of individuals)	Range (1000 × km ²)	Rank	Breadth	Position
<i>Accipiter melanoleucos</i>	W					
<i>Alcedo leucogaster</i>	W	1	2436	−28.5		
<i>Andropadus montanus</i>	E	19	53	35	102.59	0.73
<i>Andropadus tephrolaemus</i>	E	24	61	37.5	105.16	0.71
<i>Anthus cinnamomeus</i>	W	4	8787	−27	29.78	1.65
<i>Anthus trivialis</i>	W	4	10347	−29	85.58	1.73
<i>Apalis cinerea</i>	M	28	885	21.5	104.27	0.32
<i>Apalis jacksoni</i>	M	1	657	−10.5		
<i>Apalis pulchra</i>	M	29	333	34.5	104.99	0.42
<i>Batis minor</i>	W	3	3277	−19	72.07	0.97
<i>Bradypterus bangwaensis</i>	E	23	78	34	102.64	0.55
<i>Buteo auguralis</i>	W					
<i>Chloropeta natalensis</i>	W	4	3881	−16	55.9	0.94
<i>Cinnyris bouvieri</i>	W	51	1078	29.5	85.52	0.78
<i>Cinnyris reichenowi</i>	M	134	298	50	100.46	0.32
<i>Circus aeruginosus</i>	W					
<i>Cisticola brunnescens</i>	W	19	911	12.5	81.81	0.87
<i>Cisticola chubbi</i>	M	57	596	41	95.11	0.50
<i>Columba sjostedti</i>	E	1	53	4		
<i>Colius striatus</i>	W	21	7114	−7	89.63	1.12
<i>Corvus albus</i>	W	3	16987	−44	83.35	1.49
<i>Coracina caesia</i>	M	1	1130	−20.5		
<i>Corythaola cristata</i>	W	1	3329	−30.5		
<i>Cossypha isabellae</i>	E	4	61	18.5	67.89	1.13
<i>Cossypha niveicapilla</i>	W	1	5020	−34.5		
<i>Cryptospiza reichenowi</i>	M	3	841	−6	99.58	2.17
<i>Cyanomitra oritis</i>	E	20	88	31	75.26	1.02
<i>Dendropicos fuscescens</i>	W	2	11267	−39	72.15	1.26
<i>Dendropicos goertae</i>	W	4	6632	−21	63.81	1.13
<i>Elminia albiventris</i>	M	1	289	−4.5		
<i>Emberiza tahapisi</i>	W	17	11915	−19.5	87.17	0.91
<i>Estrilda astrild</i>	W	28	11628	−8.5	74.23	1.45
<i>Estrilda nonnula</i>	W	58	1165	30	92.33	0.64
<i>Euplectes ardens</i>	W	1	5931	−36.5		
<i>Euplectes capensis</i>	M	34	4538	10	79.95	0.84
<i>Euschistospiza dybowskii</i>	W	3	797	−4	59.13	1.32
<i>Falco biarmicus</i>	W					
<i>Francolinus squamatus</i>	W	5	2867	−6.5	84.44	0.76
<i>Gyps africanus</i>	W					
<i>Hirundo fuligula</i>	W					
<i>Hirundo rustica</i>	W					
<i>Jynx ruficollis</i>	W	1	1884	−25		
<i>Lagonosticta rubricata</i>	W	8	5151	−12	28.11	1.42
<i>Laniarius atroflavus</i>	E	51	43	54.5	99.98	0.40
<i>Lanius mackinnoni</i>	W	1	1411	−23.5		
<i>Linurgus olivaceus</i>	M	73	744	42	103.1	0.16
<i>Motacilla flava</i>	W	5	13860	−30.5	85.49	1.94
<i>Muscicapa adusta</i>	M	17	3636	−2.5	103.02	0.77
<i>Nesocharis shelleyi</i>	E	1	96	−3		
<i>Oriolus nigripennis</i>	W	4	1884	−8.5	53.73	1.61
<i>Parus albiventris</i>	M	7	771	9	91.08	0.99
<i>Phylloscopus trochilus</i>	W	29	16111	−2.5	93.36	0.64
<i>Ploceus baglafecht</i>	W	12	2103	−1	78.22	0.97
<i>Ploceus bannermani</i>	E	25	96	34	96.08	0.44
<i>Ploceus insignis</i>	M	4	815	1	91.68	1.98

Table 1 *continued*

Species	Status	Abundance (no. of individuals)	Range (1000 × km ²)	Rank	Breadth	Position
<i>Ploceus melanogaster</i>	M	3	710	-1	95.42	0.93
<i>Pogoniulus bilineatus</i>	W	11	7026	-13.5	94.11	0.73
<i>Pogoniulus coryphaeus</i>	M	39	447	38.5	99.58	0.17
<i>Psalidoprocne pristoptera</i>	W					
<i>Pseudoalcippe abyssinica</i>	M	36	1367	22	106.74	0.23
<i>Pycnonotus barbatus</i>	W	48	17066	-8	97.34	0.44
<i>Saxicola torquata</i>	W	62	6904	14.5	95.69	0.53
<i>Serinus burtoni</i>	M	62	482	44.5	95.69	0.38
<i>Serinus mozambicus</i>	W	25	12108	-12.5	85.51	0.68
<i>Streptopelia semitorquata</i>	W	1	13255	-50.5		
<i>Tauraco bannermani</i>	E	10	35	31	97.24	0.79
<i>Turdus pelios</i>	W	11	7675	-15.5	104.91	0.49
<i>Turtur tympanistria</i>	W	30	8200	0	111.15	0.44
<i>Urolais epichlora</i>	E	1	70	0.5		
<i>Vidua macrorhoa</i>	W	1	13991	-52.5		
<i>Zosterops senegalensis</i>	W	39	8919	1.5	99.23	0.47

Status: E, endemic in the Cameroon Mountains; M, montane species non-endemic to the Cameroon Mountains; W, species widespread throughout Africa occurring in both lowlands and highlands. Abundance: number of individuals in the study area detected using the point-count census method. Abundances of eight species of aerial feeders and raptors were not estimated because of the high probability of counting the same individuals at more than one census point. Range: area of the species geographical range (1000 km²) computed from the distributional maps in Sinclair & Ryan (2003). Rank: abundance–range–size ranking difference: the difference between ranks of a species ordered according to abundance and range size, respectively. The absolute value of this variable shows the degree of deviation of a species from the positive ARSR, while its sign indicates whether the species abundance is higher or lower than expected by range size. Breadth: local niche breadth expressing species tolerance to changes in habitat structure among census points calculated using canonical correspondence analysis (ter Braak & Šmilauer, 2002). Position, local niche position expressing the extremeness of species habitat requirements; high value indicates that a species lives in more extreme habitats than the community as a whole (Gregory & Gaston, 2000). Niche variables cannot be calculated for species detected at fewer than two census points, thus we do not provide their values for 14 species. See Methods for more detailed description of the calculation of the variables.

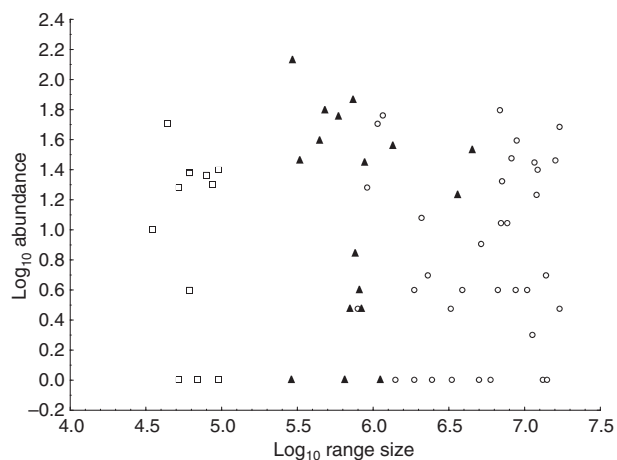


Figure 1 Interspecific abundance–range–size relationship for a bird community in the My Ogade area, Bamenda Highlands, Cameroon (Pearson $R = 0.07$, $n = 63$, $P = 0.59$). Open squares, endemic species of the Cameroon Mountains; filled triangles, non-endemic montane species; open circles, widespread species. Abundance is the total number of individuals of particular species detected using the point-count census method. Range size is in km². Both variables are log-transformed.

as habitats in the Cameroon Mountains differ considerably from the most common environments of tropical Africa (savannah woodland, arid grassland and rain forest).

To explain the observation that restricted-range species have relatively high local abundance while the widespread species have low abundance, we suggest two hypotheses concerning historical changes of the Afrotropical environment. The oscillations of global climate throughout the late Tertiary and Quaternary have caused large changes in the extent of montane forests (Newton, 2003). Montane forests were distributed widely during glacial periods but retreated into small fragments during inter-glacial periods (Jolly *et al.*, 1998; Elenga *et al.*, 2000). These fragments thus represent islands constantly occupied by montane forest during the Pleistocene (Fjeldså & Lovett, 1997a). In the mountains, the stable climatic conditions enabled the long-term persistence of montane forest, and bird species living in such an environment have had a lot of time for adaptation to local conditions. Jones *et al.* (2001) suggest that long-term adaptation to local conditions on oceanic islands could lead to high regional specialization and broad local habitat niches. This 'time to adaptation' hypothesis states that a new species that colonizes an island has low abundance and poor local adaptation. With time, it

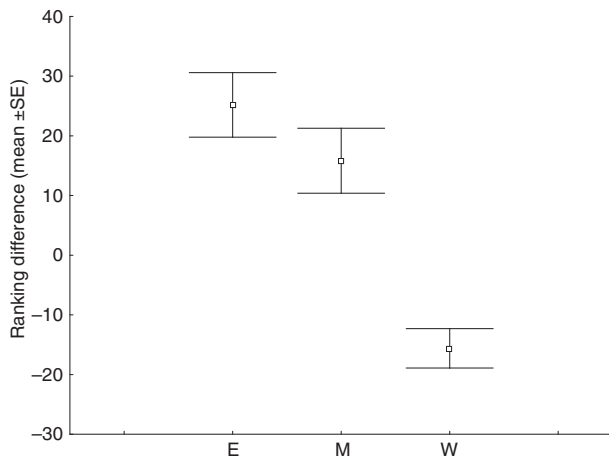


Figure 2 The abundance–range–size ranking differences in three species groups within a bird community in the My Ogade area, Bamenda Highlands, Cameroon (Kruskal–Wallis test, d.f. = 2,60; $H = 29.76$, $P < 0.001$). Abundance–range–size ranking difference is the difference between ranks of a species ordered according to abundance and according to range size, respectively. The absolute value of this variable shows the degree of deviation of a species from the positive abundance–range–size relationship, while its sign indicates whether the species abundance is higher or lower than expected by range size. E, endemic species of the Cameroon Mountains; M, non-endemic montane species; W, widespread species.

becomes more adapted and its abundance rises during the taxon cycle (Ricklefs, 1970).

In our study area, both endemic and non-endemic montane species have relatively broad niches. We suggest that, although they are able to occupy only the montane environment at the regional scale, they are well adapted to local conditions and are able to exploit a wide range of local habitats and resources in this environment. On the other hand, widespread species

occupy a wider spectrum of environments at the regional scale (e.g. different types of savanna, lowland forest clearings as well as montane environment), and have broader niches throughout their ranges than reported from the study area, but in the montane environment they apparently occupy a limited spectrum of habitats. The niche-position analysis revealed that they have a tendency (albeit not significant) to occupy marginal habitats in the study area. A possible explanation is thus that the widespread species are at the edge of their ranges in montane habitats.

Our second hypothesis suggests that species that are abundant at present had large ranges in glacial periods, but their post-glacial distribution became restricted because of montane forest retreat (the ‘range-restriction’ hypothesis). This hypothesis assumes that abundance and range size are not interconnected via population processes such as metapopulation dynamics (Hanski, 1999), which would lead to the decrease of abundances after range contraction. Instead, the wide niche breadth (Brown, 1984) and the central niche position (Gregory & Gaston, 2000) would have played a major role in maintaining high abundances and wide distribution of montane species during the times of montane forest extension. The wide local niche breadth then presumably still accounts for their high local abundance at present.

Based on our data, we cannot distinguish between these two hypotheses. However, the proposed mechanisms predict different interactions between the time of montane forest island isolation and the abundance of montane bird species. The ‘time-to-adaptation’ hypothesis predicts that montane species will have higher abundances in forest areas isolated for a longer period. According to the prediction of the ‘range-restriction’ hypothesis, the abundance of montane species would not be affected by the time of isolation of particular forest areas. A comparison of bird communities of several montane forest areas with different times of isolation would

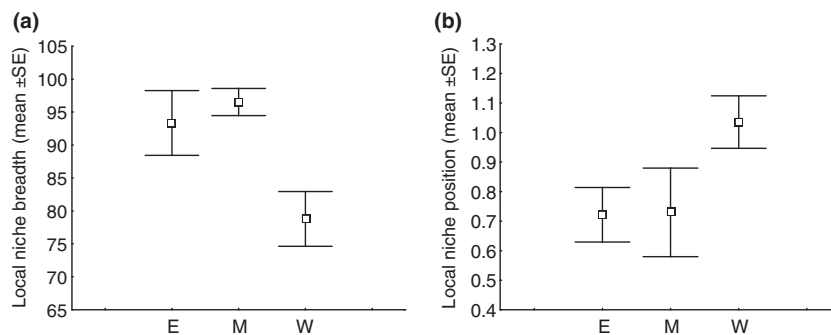


Figure 3 Differences in local niche breadth (a) and local niche position (b) between three species groups within a bird community in the My Ogade area, Bamenda Highlands, Cameroon. Both variables were calculated using canonical correspondence analysis (CCA, ter Braak & Šmilauer, 2002). Niche breadth reflects species tolerance to changes in habitat structure among census points in the study plot. Widespread species (W) have significantly narrower local habitat niches than endemic species of the Cameroon Mountains (E) and non-endemic montane species (M): ANOVA, d.f. = 2,46; $F = 6.23$, $P < 0.01$. Niche breadth is expressed as variance of CCA scores corrected by the effective number of counts. Niche position quantifies extremeness of species’ local habitat requirements with respect to the community as a whole. Widespread species use slightly more extreme habitats than endemic species and non-endemic montane species: ANOVA, d.f. = 2,46; $F = 2.53$, $P = 0.09$. Niche position is expressed in CCA scores.

distinguish between these two predictions. Nevertheless, several confounding factors could influence local abundance patterns irrespective of either hypothesis. Species' abundances could be affected by microhabitat structure (Wiens, 1989) and are expected to be lower in areas situated closer to the species' range edges (Gaston, 2003).

Exceptions can shed light on the nature of the rules. In this case, our evidence is in accordance with the notion that habitat requirements and niche properties are responsible for abundances and range sizes of species. Classical metapopulation explanations would not allow long-term persistence of species with restricted range having high abundances at the same time. Although the role of spatial population processes cannot be ruled out, the observed patterns indicate that the 'niche-breadth' explanation is probably appropriate for the reported ARSR as well as for its exceptions, at least for afro-tropical birds.

The strong adaptation of montane species to the stable conditions of montane forest could be disadvantageous for their survival in disturbed habitats. Thus one could predict that these species would be largely prone to extinction given that, during the past decades, montane forests in the Cameroon Mountains have suffered extensive habitat loss and fragmentation (Stuart, 1986). However, we found that both endemic and non-endemic montane species (including globally threatened *Tauraco bannermani*, *Ploceus bannermani*, *Andropadus montanus* and *Bradypterus bangwaensis*) are among locally common species that occupy even small forest fragments. We suggest that these species are relatively resistant to the montane forest fragmentation. It is, however, questionable whether these species could maintain long-term viable populations in such fragmented landscapes. Future research should be focused on determining the most important traits responsible for species survival in montane forest fragments, and on revealing what level of fragmentation is sustainable for the persistence of endangered species.

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