COMMUNITY ECOLOGY - ORIGINAL RESEARCH



Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: space limitation in montane forest selects for higher population densities

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Received: 29 April 2015 / Accepted: 8 January 2016 / Published online: 22 January 2016 © Springer-Verlag Berlin Heidelberg 2016

Abstract The usual positive inter-specific relationship between range size and abundance of local populations can have notable exceptions in Afrotropical montane areas, where range-restricted bird species are unusually abundant. We tested how the area occupied locally by passerines and their geographic range size relate to local abundances along a tropical elevational gradient of Mt Cameroon, West-Central Africa. Data on bird assemblages were collected at six forested elevations (350, 650, 1100, 1500, 1850 m, 2200 m a.s.l.) using a standardised point count at 16 locations per elevation. Elevational ranges of birds were compiled from published sources and their geographic range sizes were determined as the occupancy of 1° x 1° grid cells. The observed relationship between local abundance and geographic range size within the entire passerine assemblage on Mt Cameroon disagrees with the most frequently reported positive pattern. However, the patterns

Communicated by Ola Olsson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3554-0) contains supplementary material, which is available to authorized users.

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differ among elevations, with positive trends of the abundance-range size relationship in lowland changing to negative trends towards higher elevations. Interestingly, the total assemblage abundances do not differ much among elevations and population size estimates of species occupying different parts of the gradient remain relatively constant. These patterns are caused by relatively high abundances of montane species, which might be a result of long-term ecological specialization and/or competitive release in species-poor montane locations and possibly facilitated by an extinction filter. Our data suggest that montane species' abilities to maintain dense populations might compensate for less area available near mountain tops and help these populations to circumvent extinction.

Keywords Density compensation · Extinction filter · Passerines · Specialization · Tropical mountain

Introduction

Macroecological studies have revealed a pervasive positive inter-specific correlation between range sizes and abundance in local populations (Brown 1984; Gaston and Blackburn 2000; Gaston et al. 2000). Several hypotheses have been proposed to explain this pattern. In addition to methodological issues such as incomplete sampling (Bock and Ricklefs 1983; Komonen et al. 2009), mechanistic explanations include (1) resource use and availability species utilizing a wider range or more abundant resources becoming most abundant and widely distributed (Brown 1984; Hanski et al. 1993); (2) vital rates—high population growth rate leading to high abundance and more occupied sites (Holt et al. 1997); or (3) dispersal—intensive dispersal among sub-populations of individual species producing a positive inter-specific abundance-range size relationship (O'Connor 1987; Hanski et al. 1993); for review see Gaston et al. (2000) and Borregaard and Rahbek (2010).

The majority of positive abundance range-size relationships (ARSR) have been demonstrated on datasets from temperate regions and relatively few datasets on local abundances are available from tropical regions (but see Gaston 1996; Blackburn et al. 2006), where the majority of the world's biodiversity is concentrated (Willig et al. 2003). Before more comprehensive data on local abundances from tropical regions are available, some caution is warranted with respect to the shape of the inter-specific ARSR. Recently, it has been found to be systematically violated in avian assemblages in tropical montane forest environments (Reif et al. 2006; Djomo et al. 2014), where range-restricted species are generally abundant (Fjeldså 1999; Ryan et al. 1999; Sekercioğlu and Riley 2005; Hořák et al. 2010; Fjeldså et al. 2010, 2012). Factors underlying high abundances of montane forest endemics remain unknown, but several mutually non-exclusive hypotheses have been proposed:

- Long-term eco-climatic stability (especially on the mountains near thermally stable ocean currents) facilitates ecological specialization, which consequently results in high local abundances of montane species (Fjeldså et al. 2012).
- 2. High abundances of montane forest species are a result of density compensation in species-poor communities at high altitudes (MacArthur et al. 1972).
- Locally abundant tropical montane species survive despite their small range sizes, whereas insufficiently abundant species are systematically removed by an extinction filter (Johnson 1998; Williams et al. 2009).

Such mechanisms may of course act synergistically. Indeed, a high degree of ecological specialization together with less intensive inter-specific competition due to low species richness might support high population numbers in montane species and consequently help them to circumvent the extinction filter. Comparing abundance-range size patterns helps us to elucidate which mechanisms are involved in shaping the structure of tropical montane bird communities. First, the specialization hypothesis predicts that montane species should be relatively more specialized. Unfortunately, this hypothesis is difficult to test. Second, the density compensation hypothesis predicts that more niche space becomes available with decreasing species richness of bird assemblages, which leads to increased population densities of the species present. Consequently, the total number of individuals remains similar across assemblages of different elevations. Third, the extinction filter hypothesis posits that species having both small geographic ranges and low local densities are prone to extinction due to low population sizes. Thus the extinction risk is higher in island-like montane areas, between which the flow of individuals is limited (Dowsett 1986; Fjeldså and Bowie 2008; Fjeldså et al. 2010; Voelker et al. 2010). In consequence, a negative ARSR might arise in montane assemblages. A similar pattern can be expected for species occupying a small area on the mountain and having low population densities at the same time, as this increases the risk of local extinction (Shaffer 1981; Lande 1988). Higher local densities, favoured by selection due to spatial limitations on the mountain, should mitigate the effect of elevation on avian population size.

It is difficult to disentangle the role of these mechanisms, because ecological processes may operate at large as well as local spatial scales. However, initially, investigations of relationships between abundances of avian populations and area occupied by a species locally and regionally have potential to elucidate the pattern. For this purpose, a complete elevational gradient in the tropics is an ideal model system. Given the fact that most species are confined to a specific elevational band (Dowsett 1986; Romdal 2001; Price et al. 2014), the area occupied by particular species will, in general, decrease towards the highest elevations. Similarly, range sizes of species reflect their positions along the elevational gradient, with less widespread species being found at higher elevations (Fjeldså et al. 2012). Thus, by comparing area effects on local abundances of birds we can shed some light on mechanisms behind the distorted ARSR in tropical mountains (Reif et al. 2006; Djomo et al. 2014).

In this study, we focused on passerine assemblages along the elevational gradient of Mt Cameroon in West-Central Africa. The specific goals of the present study were:

- To describe changes in abundances of species occupying different parts of the elevational gradient.
- 2. To reveal how such changes affect ARSR at different elevations and across the whole elevational gradient, which has not been investigated so far.
- To examine the effects of local and regional area available for particular species on their local abundances to determine if patterns are in accordance with the extinction risk hypothesis.
- 4. To estimate population sizes on Mt Cameroon and test to what extent are higher local abundances of montane bird species compensating for smaller available area when compared to their lowland counterparts.

Materials and methods

The study was performed along the south-west slope of Mt Cameroon (Cameroon, West Africa), which is a 4095-m-high active volcano, and part of the Cameroon Volcanic Line (Fig. 1). It has a perhumid climate with the highest rainfall from late March to the beginning of November (peaking in July/September), and persistent cloud cover (Fonge et al. 2005). Its south-western slopes are to a large extent covered by tropical forest, which differs from the habitats of the surrounding lowlands (Cheek et al. 1996) due to specific hydrological regime and fertility of volcanic soils. However, the primary lowland forest below 350 m a.s.l. has been replaced by plantations or secondary forests, whereas the montane forest is compressed from above, as ongoing volcanic activity generates an abrupt treeline at ca. 2200-2300 m a.s.l. The mid-elevation forest is interspersed by extensive clearings generated by disturbances by forest elephants. For more detailed description of elevational variation in forest structure see Bussmann (2006) and Proctor et al. (2007). Due to its high degree of spatial isolation, Mt Cameroon represents a clearly defined geographical unit with specific avian assemblages (Graham et al. 2005) with two strictly endemic species and ten endemic subspecies (Gill and Donsker 2014).

Bird communities were sampled in 2011–2013 during the driest season (November-December) at six forested elevations (350, 650, 1100, 1500, 1850, 2200 m a.s.l.) using a standardised point count method (Bibby et al. 2000). Birds were recorded in the morning (6-10 a.m.) at 16 points at each elevation. The sample sites had a radius of 50 m, and were located at least 150 m apart to diminish the risk of multiple counting of individuals while remaining logistically tractable for the study. Each point was visited on 3 different days, the order of points was changed during each visit to avoid biases due to daytime, and birds were recorded in three consecutive 5-min intervals during each visit. The maximum number of individuals of a species recorded at any of these 5-min intervals was recorded as its abundance at the given point, and the sum across all 16 points as its abundance at the given elevation (hereafter "elevational abundance"). Subsequently, we averaged elevational abundances across elevations at which a species occurs to calculate the mean abundance of the species at the mountain (hereafter "mean abundance") and used this for further analyses, except for the analyses of actual bird



Fig. 1 Map of the study area with the position of our six elevational study plots marked by *black triangles*. The *inset* depicts the position of our study area within the Cameroon volcanic line indicated by the *dashed line* (adapted from Favalli et al. 2012)

communities occurring at individual elevations, where their elevational abundances were used. The aggregate abundances of birds in assemblages at a given elevation (hereafter "total abundance") were calculated as the sum of abundances of all species present. Only passerine bird species were considered in this study to minimize potential confounding effects of taxonomy and/or e.g. body mass on the studied patterns. Furthermore, visitor migrants and aerial feeders (*Phylloscopus* warblers and swallows, Hirundinidae) were also excluded from this study. The taxonomy used in this study followed the International Ornithological Congress World Bird List version 4.2 (Gill and Donsker 2014).

A distance sampling protocol was used, with birds recorded in five 10-m-wide radial distance bands (Buckland et al. 2001). Here, we utilized the Distance version 6.2 software (Thomas et al. 2010) to account for differences in species detectability and to estimate the number of unobserved individuals based on fitted detection functions (Buckland et al. 2001). Application of detection adjustments is, however, generally problematic in tropical environments (Banks-Leite et al. 2014) and we used the observed abundance estimates instead of the distance sampling-based estimates in further analyses for the following reasons:

- There were too few records for rare species (out of 108 species 49 were detected less than ten times) for detection functions to be fitted and reliable abundance estimates to be retrieved; these naturally scarce species, however, cannot be simply omitted from our analyses.
- 2. Our estimates derived from distance sampling were highly correlated with the observed abundance estimates (Spearman's $\rho = 0.42$, n = 59, p < 0.001; Electronic supplemental material Appendix 1, Fig. A1.1).
- Exceptions exist for which abundance estimates based on detection functions are unrealistically high (see Appendix 1 in Electronic supplemental material for further details).
- 4. Additional analyses run for a subset of species for which there were at least ten observations [although generally at least 60–80 observations are recommended (Buckland et al. 2001)] did not indicate that the results are sensitive to the type of abundance estimates used (see Electronic supplemental material Appendix 1, Fig. A1.2, A1.3).

Data on elevational ranges of passerines were compiled from primary published sources containing exact elevational observations or altitudinal limits recorded for each bird species on Mt Cameroon (see Electronic supplemental material Appendix 2 for references). The elevational midpoint was calculated from the lower and upper altitudinal limit of a species distribution on Mt Cameroon. Species were divided into three exclusive groups according to the position of their elevational midpoint as follows: (a) species having their elevational midpoint in the lower third of the elevational gradient (up to 800 m a.s.l.) were included in the "lowland" group, (b) species with midpoints between 800 and 1600 m a.s.l. comprised the "middle" group, and (c) species with their midpoint in the upper third of the gradient (above 1600 m a.s.l.) represented the "montane" species group. The classification approximately reflects distinct vegetational zones on Mt Cameroon.

The global species' range sizes were determined as the occupancy of $1^{\circ} \times 1^{\circ}$ grid cells where a species breeds or is resident (Rahbek et al. 2012). Mt Cameroon was divided into 100-m elevational bands and the area of each band was calculated using the GMTED2010 dataset provided by the US Geological Survey (http://earthexplorer.usgs.gov/). The local area on Mt Cameroon potentially occupied by individual species was calculated as the summed area of elevational bands that each species occupies. Subsequently, the extrapolated population size of each species on the mountain was calculated as the product of its recorded mean density on Mt Cameroon and local area occupied.

Non-parametric Spearman-rank correlation analysis was utilized to describe the relationship between local abundance and range size or local area occupied by a species. Differences in abundances, range sizes, local area occupied and extrapolated population sizes of species having their midpoints in lowland, mid-elevations or montane environment were analysed by means of a non-parametric Kruskal–Wallis test.

Results

Altogether 108 passerine species were recorded at study plots (excluding visitor migrants and aerial feeders; see "Materials and methods" for further details). The mean abundance (calculated as the average of elevational abundances across occupied elevation) of individual species ranged from one to 48.33 (median = 7.71) and increased with the midpoint of their elevational distribution (Spearman's $\rho = 0.38$, p < 0.001). The global range sizes spanned from one 1°×1° grid cell to 1081 grid cells (median = 152.50) and decreased with the species' elevational midpoint ($\rho = -0.44$, n = 108, p < 0.001). The local area potentially occupied by each species on Mt Cameroon also decreased with its elevational midpoint ($\rho = -0.40$, n = 108, p < 0.001). Species having their elevational midpoint in the montane forest (above 1600 m a.s.l.) had the highest mean abundances (Fig. 2a; Kruskal-Wallis χ^2 15.11, df = 2, p < 0.001), but the lowest range sizes (Fig. 2b; Kruskal–Wallis χ^2 30.19, df = 2, p < 0.001) and



Fig. 2 Passerine species divided into three groups based on the position of their midpoint of elevational distribution on Mt Cameroon (see "Materials and methods"): a mean abundance of individual species across elevations (Kruskal–Wallis χ^2 15.11, df = 2, p < 0.001);



Fig. 3 Total abundances and number of individuals per species for particular bird assemblages along the elevational gradient on Mt Cameroon

Fig. 4 a Abundance-range size relationship of passerine species occurring along the elevational gradient of Mt Cameroon (Spearman's $\rho = -0.16$, n = 108, p = 0.1). b Abundance-local area relationship ($\rho = -0.10$, n = 108, p = 0.31). Note log scale used on *x*-axes and square-root transformation on *y*-axes. *Grey triangles* represent endemic species or sub-species **b** range size = number of occupied $1^{\circ} \times 1^{\circ}$ grid cells (note log scale used on *y*-axis; Kruskal–Wallis χ^2 30.19, df = 2, p < 0.001); **c** local area (km²) occupied on Mt Cameroon (note log scale used on *y*-axis; Kruskal–Wallis χ^2 30.81, df = 2, p < 0.001)

occupied the smallest area locally on the mountain (Fig. 2c; Kruskal–Wallis χ^2 30.81, df = 2, p < 0.001).

The total abundances of birds in focal assemblages were relatively similar along the elevational gradient, reaching values of ca. 430–470 individuals at 16 sampling points. Exceptions were the lowest elevation of 350 m a.s.l. harboring only 320 individuals, and the elevation of 1100 m a.s.l. with the most abundant bird community having a little less than 600 individuals (Fig. 3, dark bars). The number of individuals per species increased continually with altitude, with approximately three times as many individuals per species at the highest elevation as in the lowland (Fig. 3, light bars).

The ARSR across all species of the entire forested elevational gradient of Mt Cameroon showed a negative albeit non-significant trend ($\rho = -0.16$, n = 108, p = 0.1; Fig. 4a). The signature of an extinction filter, if it operates, should be most pronounced in endemic species and subspecies (highlighted as grey triangles in Fig. 4) as they have no or limited possibilities of recolonization from other





Fig. 5 Abundance-range size relationships of three groups of passerine bird species: **a** species with midpoints below 800 m a.s.l. (Spearman's $\rho = 0.40$, n = 56, p < 0.01); **b** species with midpoints between 800 and 1600 m a.s.l. ($\rho = -0.30$, n = 33, p = 0.1); **c** species with midpoints above 1600 m a.s.l. ($\rho = -0.03$, n = 19,

Table 1 Non-parametric Spearman rank correlations (ρ) between abundance of passerines and their geographic range size (*ARSR*), and locally occupied area (*Abundance-local area*) on Mt Cameroon

Elevation	п	ARSR		Abundance-local area	
		ρ	р	ρ	р
"Lowland"	56	0.40	<0.01	0.26	<0.1
"Middle"	33	-0.30	0.1	-0.02	0.9
"Montane"	19	-0.03	0.92	0.64	< 0.01
350 m	53	0.39	< 0.01	0.36	< 0.01
650 m	61	0.26	< 0.05	0.17	0.18
1100 m	52	-0.20	0.15	-0.07	0.65
1500 m	34	-0.40	< 0.05	-0.13	0.45
1850 m	32	-0.37	< 0.05	0.10	0.59
2200 m	21	-0.14	0.54	0.12	0.6

areas. Unfortunately, their low sample size does not allow for proper statistical testing. In contrast with the ARSR of all species along the entire elevational gradient, the ARSR of the three species groups with different elevational midpoints showed a variable pattern, as it changed from a positive trend in the lowland group, to a negative, but non-significant trend for middle species, and no trend for montane species (Fig. 5a–c respectively; Table 1). A similar pattern was found for passerine assemblages at different elevations as it changed from a positive trend in the lowland (350 m and 650 m a.s.l., Electronic supplemental material Appendix 3, Fig. A3a, b; Table 1) to a negative or no trend at higher elevations (Fig. A3c, d, e, f; Table 1). On the contrary, no trend in abundance-local area relationship was revealed across the entire elevational gradient ($\rho = -0.10$,

p = 0.92). Trends are depicted by regression lines fitted by the ordinary least squares method. Note log scale used on *x*-axes and square-root transformation on *y*-axes. The *insets* depict the patterns we expected for particular species groups based on range size limitations and increasing abundance towards higher elevations



Fig. 6 Extrapolated population sizes (mean density \times area occupied locally) of detected passerine bird species on Mt Cameroon (note log scale used on *y*-axis; Kruskal–Wallis χ^2 0.66, df = 2, p = 0.72)

n = 108, p = 0.31; Fig. 4b). The trend was positive in lowland and montane species, whereas no trend was detected in middle species (Table 1). Within assemblages at individual elevations a positive trend was detected at the lowermost elevation, but was insignificant elsewhere (Table 1).

The extrapolated population sizes for individual passerines on Mt Cameroon did not differ among the three groups of species classified according to the position of their elevational midpoint (Kruskal–Wallis $\chi^2 0.66$, df = 2, p = 0.72; Fig. 6). The predictions of hypotheses considered in this study along with whether the observed patterns are in congruence with them is summarized in Table 2.

Hypothesis	Predicted pattern	Congruence with observed patterns
Density compensation	Species' population densities increase with decreasing species richness of assemblages	Yes (Fig. 2)
	Total number of individuals is similar across assemblages with different species richness	Yes (Fig. 2)
Specialization	Higher specialization of montane species	Not tested
Extinction filter	Species having both small geographical ranges and low local densities are prone to extinction due to low population sizes and are thus missing from assem- blages => negative ARSR at higher elevations	Partial (Fig. 5, Fig. A3)
	Species occupying a small area on the mountain and having low local densities are prone to extinction due to low population sizes and are thus missing from assemblages => negative trend of abundance-local area at higher elevations	No (Table 1)
	Independence of population sizes on the elevational zone occupied by species	Yes (Fig. 6)

 Table 2
 Summary of predictions of hypotheses explaining high abundances of tropical montane bird species and their congruence with patterns observed in this study

Discussion

In this study, we tested for the first time the abundancearea relationship in passerine assemblages along a tropical elevational gradient. We found a negative (though non-significant) relationship between local abundance and range size at the scale of the whole mountain, which contradicts a positive trend frequently observed in temperate regions (Gaston and Blackburn 2000). Deviation from a positive ARSR is obviously caused by a combination of decreasing range sizes and increasing abundances of birds towards high elevations, as the montane range-restricted species turned out to be the most abundant ones, in agreement with several previous studies (Fjeldså 1999; Ryan et al. 1999; Sekercioğlu and Riley 2005; Reif et al. 2006; Fjeldså et al. 2010, 2012; Djomo et al. 2014).

Avian species richness declines monotonically with elevation on Mt Cameroon (Hořák et al., unpublished data), which is a typical pattern for wet-based mountains (McCain 2009), and we show here that the number of individuals per species increases with elevation. Such an observation fits to predictions of the density compensation hypothesis, which suggests that in species-poor assemblages individual species may increase their abundances to fill the available free ecological space (MacArthur et al. 1972). Our data suggest "an exact compensation" as the total abundances of bird assemblages in montane elevations were similar to those of lower ones. Only the lowest (350 m a.s.l.) and midelevation (1100 m a.s.l.) deviated notably from the typical values. This is an interesting fact considering that overall environmental productivity (McCain 2009) and food availability as estimated by abundance of insects or fruits seem to decrease with altitude (Janzen 1973; Janzen et al. 1976; Loiselle and Blake 1991). Thus, one would expect elevational decrease in total abundances, too. However, the food limitation issue remains poorly studied along tropical

elevational gradients, and the productivity gradient might be relatively shallow on this extremely wet and warm tropical mountain. Moreover, availability of food to birds can be significantly influenced by variation in environmental seasonality along elevations, about which we do not have much information so far. The uniform abundance pattern could also be explained by fine specializations of montane species to habitats at high elevations, allowing them to reach total abundances comparable to those of more diverse communities (Diamond 1970; MacArthur et al. 1972; Wright 1980). Nevertheless, the extent to which competitive release and density compensation can account for high abundances of montane species remains to be evaluated within guilds of competing species (Wright 1980).

In addition, we found differences in ARSR between elevations. For the lowland forest assemblage (350 m and 650 m a.s.l.) the ARSR was positive, while it was negative at mid-elevations (1500 m and 1850 m a.s.l.), and no trend was revealed at 1100 m a.s.l. and in the upper montane forest (2200 m a.s.l.). The same qualitative patterns emerged for groups of species defined according to the position of their elevational midpoint, with positive ARSR in the lowland group, a non-significant negative trend of ARSR in the middle group and no trend in the montane species. These findings imply two important points. First, the overall ARSR across all species occurring on the elevational gradient of Mt Cameroon is not a single relationship, but is composed of multiple forms of ARSR occurring along this steep environmental gradient (cf. Gaston 1996; Blackburn et al. 2006). Second, they suggest that the unusual ARSR, as reported for some tropical environments, may be an idiosyncrasy of montane (or other insular) environments rather than a general feature of tropical bird assemblages, because lowland patterns follow the expectations based on the most frequently observed patterns. The density compensation hypothesis alone is unable to fully account for the diversity

of ARSRs detected, as it does not make any predictions about differential effects of range sizes within individual elevational assemblages. We propose that interactions of several factors are responsible. Specifically, a combination of missing range-restricted species in lowland areas, and increased densities (facilitated by ecological specialization and/or density compensation) in species of upper elevations coupled with their small ranges creates the observed elevational changes in ARSR.

Basically, small range sizes of Afromontane bird species select for high local abundances, which lower their risk of extinction, as has been suggested for marsupials in Australia (Johnson 1998), birds of the Australian wet tropics (Williams et al. 2009) or butterflies in Finland (Komonen et al. 2009). Such a hypothesis ultimately assumes that extinction filters remove small-range species that have scarce local populations. This mechanism could account for elevational differences in ARSR described here, as its effect should be more pronounced towards higher elevations, where factors influencing risks of extinction, i.e. the area occupied locally and range sizes (Shaffer 1981; Lande 1988) tend to decrease. The extinction risk hypothesis further predicts a relatively stronger effect of local area on abundances, when compared to range size, because of its more direct effect on local populations. Contrary to our expectations, we observed none and positive relationships between area occupied locally and abundance in passerine assemblages on Mt Cameroon. Moreover, a non-significant pattern observed in the uppermost bird assemblages, where the effect of an extinction filter should be the strongest, does not fit to the extinction risk hypothesis. Nevertheless, the extinction hypothesis should not be discarded, as the estimated population sizes of individual bird species on Mt Cameroon did not change with their elevational midpoint. It suggests that high abundances of species living at upper elevations compensate for area reduction towards higher altitudes, so that overall population sizes of montane birds remain on average similar to population sizes of species at low elevations (Fig. 6). Small populations of montane species would presumably raise their extinction risk significantly (Lande 1988; Purvis et al. 2000).

In conclusion, we found that the distorted ARSR in an avian assemblage on Mt Cameroon is mostly a result of relatively high local abundances of species at high elevations. At the same time it is not a single relationship, and bird assemblages inhabiting different elevations show contrasting shapes of ARSR. Our data imply that high abundances of montane passerines might compensate for the small areas available at high elevations, and as a result they can maintain population sizes comparable to those of their lowland-forest counterparts. This pattern might partly be an outcome of an extinction filter which favours tropical montane forest species that are able to attain high local abundances by means of specialization or by taking advantage of local environments with less intensive competition.

Acknowledgments We wish to thank the communities of Bokwango and Bakingili villages for their support during the fieldwork. We are grateful to Francis Luma for fieldwork management. We thank the Department of Environmental Sciences of the University of Buea, Cameroon and in particular Eric Fokam, Philip Tem Dia, Philip Ngafor and Bertilla Sirri for their assistance during the fieldwork, and Jana Vokurková and Andrew Reeve for stimulating comments on earlier drafts of this manuscript. Tomáš Albrecht and David Storch helped us during point counts. We also thank Kevin Njabo and the IRTC of the University of California, Los Angeles in Yaoundé for their technical support. This study was performed with the authorisation no. 0104/PRBS/MINFOF/SG/DFAP/SDVEF/SC of the Ministry of Forestry and Wildlife of the Republic of Cameroon and with the support of Mt Cameroon National Park authorities. The research was funded by the Czech Science Foundation (project no. P505/11/1617), and J. F. acknowledges the Danish National Research Foundation for support to the Centre for Macroecology, Evolution and Climate.

Author contribution statement D. H., M. F., J. F. and O. S. conceived the ideas; D. H., O. S., F. N. M., E. D. N., M. F. and K. M. collected the data; M. F. performed the statistical analysis; M. F., D. H. and J. F. wrote the manuscript; O. S. and E. D. N. contributed to the writing.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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