JOURNAL OF
AVIAN BIOLOGY

Research Article

The abundance-centre hypothesis re-examined: body mass, blood glucose, and elevational distributions in Afrotropical forest birds

Riccardo Pernice[1], Tomáš Albrecht[2,3], Oldřich Tomášek[2,3], Ondřej Kauzál[2,3], Francis Teke Mani[4], Esembe Jacques Chi[4], Matouš Janča[2,5], Vincenzo Arizza[6], Daniela Campobello[6] and David Hořák[1]

[1]Charles University of Prague, Department of Ecology, Faculty of Science, Viničná, Prague, Czech Republic
[2]Czech Academy of Sciences, Institute of Vertebrate Biology, Květná, Brno, Czech Republic
[3]Charles University of Prague, Department of Zoology, Faculty of Science, Viničná, Prague, Czech Republic
[4]Bokwaongo Ornithological Club, Buea, Cameroon
[5]Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská, Brno, Czech Republic
[6]Dipartimento di Scienze e Tecnologie Biologiche, Chimiche e Farmaceutiche (STEBICEF), Università di Palermo, Palermo, Italy

Correspondence: Riccardo Pernice(pernicer@natur.cuni.cz)

Journal of Avian Biology
2026: e03612
doi: 10.1002/jav.03612

Subject Editor: Elisa Bonaccorso
Editor-in-Chief: Jan-Åke Nilsson
Accepted 26 June 2026

A long-standing theory, the abundance-centre hypothesis (ACH), predicts that species peak in abundance at the centre of their geographic range, where environmental conditions are optimal, and decline towards range limits as conditions deteriorate. Yet, tests of the ACH in birds along elevational gradients have yielded mixed results. Moreover, resource availability, rather than abiotic factors per se, may better explain species abundance patterns. Therefore, life-history traits associated with nutritional status could be key to predicting abundance patterns. Along with the ACH, we tested two physiological traits as potential predictors of avian abundance along an Afrotropical elevational gradient: blood glucose concentrations (the abundance–glucose relationship; AGR) and body mass (the abundance–body mass relationship; ABR). We collected abundance, glucose, and body mass data from 51, 15, and 29 free-living species, respectively, within a primary forest on Mt Cameroon (West-Central Africa). Model fits for each species revealed that many species show a monotonic abundance pattern. Logistic models further indicated that high-elevation birds were more likely to increase in abundance with elevation, peaking near the treeline. In contrast, lowland birds tended to decline with elevation, peaking near the lower forest edge. Bayesian phylogenetic multilevel models indicated that neither glucose nor body mass was a strong predictor of abundance. Taken together, our findings provide little support for the ACH and suggest that most lowland and highland species occupy truncated realized niches near forest elevational edges. Although our results do not link avian physiology to population density, we encourage future ecologists and ornithologists to collect larger sample sizes to effectively test the AGR and ABR hypotheses and, thus, elucidate the mechanisms behind variations in species abundances.

Keywords: abundance-centre hypothesis, avian physiology, blood glucose, body mass, elevational gradient, habitat barriers, truncated niche

NORDIC SOCIETY OIKOS

www.avianbiology.org

Introduction

Understanding how species distribution and abundance vary across space is a central question in ecology, as it is essential for developing theoretical models and refining conservation efforts (Gaston 2003). A long-standing biogeographical concept, known as the abundance-centre hypothesis (hereafter ACH), posits that species are typically most abundant near the centre of their geographical range and become steadily rarer towards the edges of their distribution (Darwin 1876, Brown 1984, Brown et al. 1995). This hypothesis is based on the idea that ecological conditions near the centre of the range are optimal and deteriorate towards the range boundaries (i.e. symmetric distribution; Hengeveld and Haeck 1982, Brown 1984, Sagarin and Gaines 2002). Although the ACH is considered a fundamental rule in biogeography (Hengeveld and Haeck 1982), empirical studies have provided mixed support, with species abundance distributions showing varying patterns along environmental gradients (e.g. flat, monotonic, or skewed) (Austin 2002, Oksanen and Minchin 2002, Sagarin and Gaines 2002, Freeman and Beehler 2018). These contrasting abundance patterns may result from different abiotic and biotic factors, including abiotic stress, parasitism, predation pressure, interspecific competition, or even the absence of a clear climatic optimum across the gradient (Diamond 1973, Hunt and Scheibling 1998, Sagarin et al. 2006, Borregaard and Rahbek 2010, Tam and Scrosati 2011, Burner et al. 2019). In addition to abiotic and biotic factors, physical habitat barriers may also explain abundance patterns along environmental gradients. For example, abrupt transitions between habitat types may constrain species distributions independently of climatic tolerances (Terborgh 1977, 1985, Neate-Clegg and Tingley 2023). Under such conditions, species abundance patterns may deviate from the symmetric distribution predicted by the ACH, potentially resulting in monotonic or skewed abundance distributions toward range limits because habitat boundaries may occur before species reach the full extent of environmental conditions they can tolerate (Feeley and Silman 2010, Freeman and Beehler 2018).

The underlying rationale of ACH is that species abundances reflect how well an area fulfils species' ecological needs across multiple niche axes (Brown 1984). When these axes are defined by abiotic variables, it may be argued that species distribution and population density are limited by factors that influence organisms' physiological tolerances (Janzen 1967, Burner et al. 2019). However, it might be more precise to say abiotic factors gain significance primarily because they indirectly influence other environmental parameters, such as the availability of food resources, which ultimately determine the number of individuals that can persist in a given area (Virgós et al. 2011, Ferger et al. 2014, Sam et al. 2019). Indeed, it is reasonable to believe that even in areas offering ideal climatic conditions, a species' persistence cannot be guaranteed if food availability declines (e.g. because of interspecific competition; Luiselli 2006, Braz et al. 2020). From this perspective, food availability emerges as a crucial driver of population density growth (cf. food limitation hypothesis, Lack 1947), supporting the idea that patterns in species abundance should mirror those in food availability. This remains true regardless of whether species abundance distributions follow a symmetric pattern, a monotonic one, or another form.

Estimating spatial variation in food availability and species abundance can be time-consuming and costly, especially when fieldwork involves remote, poorly studied regions. A practical alternative, when direct food supply estimates are lacking, is to use measurable in situ traits linked to spatial variation in food quantity (Blackburn et al. 1999). For example, Virgós et al. (2011) inferred the distribution and quality of food availability for European badgers by measuring body and skull size of individuals along a latitudinal gradient. The authors reasoned that individuals were largest and heaviest where food availability and quality were highest. In turn, being large may enable an organism to acquire a higher proportion of resources, which leads to the organism thriving in a given area (White et al. 2007, Gaston and Blackburn 2008). On the other hand, when the availability of resources is limited, smaller organisms may occur in higher numbers than larger ones, as the latter need more energy to fuel their metabolism (Damuth 1981, Cermeño et al. 2006, White et al. 2007, Roberts et al. 2024). In general, the direction of the abundance–body mass relationship (ABR) remains ambiguous, with studies reporting both positive and negative associations (Silva and Downing 1995, White et al. 2007, Hu et al. 2021). Temperature may further shape this relationship, with larger-bodied species tending to be more abundant in colder environments and smaller-bodied ones in warmer climates (James 1970, Salewski and Watt 2017; Table 1). Despite these complexities, life-history traits remain valuable for uncovering ecological drivers of abundance patterns and can be complemented by other physiological traits responsive to abiotic conditions (Ricklefs and Wikelski 2002).

Many organisms regulate their physiology to maintain energy balance in response to food availability (McCue 2010). Under food scarcity, this often involves mobilizing internal energy reserves. Glucose, a key metabolic carbohydrate, is commonly used as an indicator of energy balance and starvation (Larsen et al. 1985, Scanes and Braun 2013, Schradin et al. 2015, Tomášek et al. 2019). Chronic food restriction has been linked to reduced blood glucose levels across taxa, including small mammals (Rimbach et al. 2017), amphibians (Smith 1950), and birds (Alonso-Alvarez and Ferrer 2001). Collectively, these findings suggest that blood glucose may serve as a proxy for environmental quality and, thus, a potential predictor of species abundance. However, glucose variation across space remains poorly understood in wild animals, even in well-studied groups like birds. One exception is Tomášek et al. (2022), who found that baseline glucose levels in passerines increase with elevation, likely due to greater energy demands or higher reliance on carbohydrates in colder, low-oxygen environments. Alongside other studies (Fokidis et al. 2012, Vágási et al. 2020), this points to blood glucose as a physiological marker not only of energy

Table 1. Hypotheses and the resulting ecological outcome for abundance-centre hypothesis (ACH), abundance–glucose relationship (AGR), and abundance–body mass relationship (ABR) along the elevational gradient of Mt Cameroon.

Ecological relationship	Hypothesis	Outcome
ACH	Species tend to be more abundant in the centre of their elevational distribution as a reflection of optimal environmental conditions (Freeman et al. 2018).	Highest species abundances in the centre of their elevational ranges. Consequently, abundance distributions are statistically well described by symmetric bell-shaped curves.
AGR	Population density tends to be higher where resources are abundant. If blood glucose reflects energy balance, individuals in resource-rich environments should also exhibit higher glucose levels.	Positive AGR
	Population density declines under harsh conditions. If glucose reflects physiological stress, species or individuals in stressful environments (e.g. low temperatures) should show elevated glucose levels (Tomášek et al. 2022).	Negative AGR| Significant interaction between elevation and circulating glucose concentrations in predicting abundance.
ABR	Where resources are abundant, species tend to be more abundant. Individuals in such favourable conditions are expected to have greater body mass, reflecting their ability to accumulate energy for growth (Virgós et al. 2011).	Positive ABR
	Where the level of resources is moderate, species abundance peaks are driven by small-bodied individuals, as they need less energy to fuel their metabolism (Damuth 1981).	Negative ABR
	In cold environments, large-bodied species tend to be more common than smaller species, as they are able to retain heat more efficiently (Mayr 1956).	Significant interaction between body mass and elevation in predicting abundance.

status but also of environmental stress. Thus, it may serve as a powerful proxy for both food availability and environmental harshness. If spatial patterns of species abundance correlate with glucose levels, high abundance paired with low glucose may indicate favourable conditions, whereas declining abundance alongside elevated glucose may reflect significant stress (Table 1). Despite its promise, this abundance–glucose relationship (AGR) remains largely unexplored and merits further investigation.

To test the abovementioned hypotheses, examining species abundance patterns across ecological gradients, such as mountain slopes, offers a practical and effective approach. Mountains have long served as natural laboratories for exploring ecological relationships involving abundance and distribution (Reif et al. 2006, Wen et al. 2018a, 2018b, Hořák et al. 2019). Elevational gradients are especially valuable because abiotic variables tend to change predictably with altitude, in contrast to the multidirectional variation found along latitudinal or longitudinal gradients (Sagarin and Gaines 2002). Additionally, the relative habitat continuity along slopes minimizes dispersal barriers (but see Janzen 1967), facilitating standardized sampling (Burner et al. 2019, Santini et al. 2019, Wen et al. 2021. These features make elevational gradients well-suited for disentangling ecological drivers of abundance. Yet, despite their advantages, direct tests of these hypotheses remain limited: the ACH has been addressed in only a few studies with mixed outcomes (Freeman and Beehler 2018, Burner et al. 2019), the ABR has been rarely explored (Hu et al. 2021), and the AGR remains entirely untested. In this study, we used the most comprehensive dataset to date on the abundance of forest bird species along the elevational gradient of Mt Cameroon (West-Central Africa; Sedláček et al. 2023), ranging from 350 m a.s.l. to the treeline (~2300 m a.s.l.), to test the predictions of the ACH and examine the relationship between species abundance and blood glucose (AGR) and body mass (ABR). Our goals were to 1) test whether species were relatively abundant at the centre of their elevational range and rare at their range limits, 2) determine whether blood glucose and body mass predict their abundance patterns, and 3) explore how their effects vary with elevation under differing abiotic conditions. Relevant hypotheses and a priori predictions for the abundance-based relationships along the elevational gradient of Mt Cameroon are shown in Table 1.

Material and methods

Study area and abundance dataset

Mount Cameroon is the highest peak in West and Central Africa and part of the Cameroon Volcanic Line chain stretching from the Gulf of Guinea (volcanic islands Bioko, Sao Tome, Principé) to northern Cameroon (Marzoli et al. 2000). Mount Cameroon is an active volcano and an important hotspot of biodiversity on a global scale (Küper et al. 2004). The south-western slope of the mountain is covered by a continuous forest gradient, from approximately 350 m to the treeline (ca 2300 m a.s.l.). At intermediate elevations (1000–1500 m a.s.l.), the forest experiences natural disturbances due to the presence of local African forest elephant *Loxodonta cyclotis* populations (Maicher et al. 2020a, Kamga et al. 2022). Mount Cameroon exhibits conspicuous seasonality. In the wet season, monthly precipitation exceeds 2000 mm in certain areas, while during the dry season, precipitation is almost completely absent (Maicher et al. 2020b).

We used abundance data from records of breeding birds along the southwestern elevational forest gradient of Mt Cameroon published by Sedláček et al. (2023). The dataset

was described in detail in Sedláček et al. (2023) and is here briefly presented. Data were collected during the dry season using a standardized point-count method (Bibby et al. 2000), supplemented by random walks to detect the occurrence of rare species. For the present study, we employed abundance data collected in 2011–2015 at six forested elevations (350, 650, 1100, 1500, 1850, 2200 m a.s.l.). To test the generality of the abundance-centre hypothesis, we retrieved abundance data from species with a broad elevational distribution; that is, species detected in at least three elevations. Birds of prey were excluded from this analysis, as they have large home ranges, and it is difficult to link them to particular forest locations. In total, our dataset included 51 species and 4443 individuals.

Glucose and body mass measurements

Glucose data were collected at 350, 650, 950, 1100, and 2200 m a.s.l. along the southwestern slope of Mt Cameroon in 2013–2023. Data collected at 950 and 1100 m a.s.l. were pooled together, as there is no drastic difference between these two elevations in environmental conditions based on field observations. Additionally, we collected glucose data from birds captured around 1500 m a.s.l. in a relatively undisturbed rainforest on the southeastern slope of the mountain in 2019. Adult birds were mist-netted, and blood samples were taken from the jugular vein within 3 min after the bird was captured (mean time 105 s, range 40–180 s). Blood glucose concentrations were measured using FreeStyle Freedom Lite portable glucose metres (Abbott Diabetes Care), which have a linear range of 1.1–27.8 mmol l^{-1} (Breuner et al. 2013, Tomášek et al. 2019). To reduce the effect of seasonality, only measurements collected during the dry season were considered. Following blood sampling, we measured birds' body mass to the nearest 0.1 g using digital scales. Birds were released following the measurements.

Statistical analyses

To test whether species are most abundant at the centre of their elevational distribution and relatively rare at their range limits, we fitted seven Huisman-Olff-Fresco (HOF) models – flat, monotonic, plateau, symmetric, skewed, bimodal (skewed), and bimodal (symmetric) – to the abundance data of each species (n = 51), using the package 'eHOF' (Jansen et al. 2022) in R (www.r-project.org). For fitting the HOF models, we transformed the absolute abundances into 'relative abundance', obtained by dividing, for each species, the number of individuals recorded at a given elevation by the total number of individuals. We selected the best-fitting model for each species by bootstrapping the models 999 times and choosing the most parsimonious model based on the Akaike information criterion corrected for small datasets (AICc; Burnham and Anderson 2004). We then plotted model predictions to visualize the shape of the best-fitting models. Symmetrical curves were considered consistent with the abundance-centre hypothesis.

Next, we classified species according to the shape of their monotonic abundance–elevation curves. Species showing monotonically increasing abundances towards their upper range limit were categorized as the 'increasing' group, whereas those showing monotonically decreasing abundances towards their lower range limit were categorized as the 'decreasing' group. To test whether the probability of truncation varies along the elevational gradient, we fitted two separate binomial generalized linear models (GLMs) with logit link functions. The first model contrasted the increasing group against all other categories (i.e. monotonic decreasing and other abundance patterns), and the second model contrasted the decreasing group against all other categories (i.e. monotonic increasing and other abundance patterns). Predicted probabilities were obtained from each model, in which the predictor was the species' elevational range midpoint [(upper range limit + lower range limit)/2].

Some studies testing the relationship between circulating glucose and body mass have found a significant negative relationship (Tomášek et al. 2019, Szarka and Lendvai 2024). Thus, to explore the relationship between blood glucose concentration and body weight, we fitted a generalized linear mixed model where the response variable was blood glucose, and the predictors were log-transformed body mass, elevation, and their interaction, with a random intercept for species identity. We considered the interaction to ensure that elevation did not influence the relationship between body mass and glucose. Nevertheless, we found that neither the relationship between blood glucose and body mass nor the effect of the interaction between body mass and elevation was significant (body mass: $F_{1,\ 48.26} = 0.003$, $p > 0.05$; body mass × elevation: $F_{1,\ 370.54} = 0.09$, $p > 0.05$). This result is consistent with a previous analysis based on a much larger comparative dataset of tropical bird species, which likewise found no evidence for a relationship between blood glucose and body mass (Tomášek et al. 2022). We therefore analysed the relationship between species abundances and glucose (see below) without controlling for body mass. For this analysis, we included all glucose measurements from species sampled at a minimum of two elevations, with at least two individuals per elevation (n = 15 species, n = 431 individuals). In this subset, species-specific glucose concentrations at each elevation were calculated by averaging all glucose measurements collected for each species at that elevation.

Similarly, to test the relationship between species abundance and body mass (below), we considered all body mass measurements from species sampled at a minimum of two elevations, with at least two individuals per elevation. In total, this subset included 29 species and 1526 individuals. As for blood glucose, mean body mass was calculated for each species at each elevation and used in the subsequent abundance-body mass analyses. For both the abundance-glucose and abundance-body mass analyses, we converted absolute abundances at each elevation to within-species proportions. These analyses included a very small number of cases in which a species was captured for physiological sampling at an elevation where it was not detected in the abundance dataset (one species in the glucose dataset and two species in the body mass dataset). In these rare cases, abundance values

equal to zero were replaced with a small constant (1e-10) to avoid numerical issues in the following analyses.

We assessed whether species proportional abundances are predicted by 1) blood glucose concentrations and 2) body mass, and whether variation in abundance is further explained by 3) the interaction of glucose with elevation and 4) the interaction of body mass with elevation. Before model fitting, we log10-transformed and centred glucose and body mass. We fitted these models using Bayesian multilevel models through the 'brms' package in R (Bürkner 2017). Relative abundance was modelled using a gamma distribution with a *log-link* function. To account for phylogenetic non-independence among species in our models, we included phylogeny as a random effect, with a covariance matrix calculated from an ultrametric phylogenetic tree using the function *vcv.phylo* in the R package 'ape' (Paradis et al. 2004). Ultrametricization was performed with *force.ultrametric* function (Revell 2011) in R. We generated the ultrametric phylogenetic tree using 1000 random trees based on the 'Ericson all species: a set of 10 000 trees with 9993 OTUs each backbone (Jetz et al. 2012) from the BirdTree.org (http://birdtree.org/) platform.

To capture species-level variation in trait–abundance relationships, we specified models with random intercepts and random slopes for each species for the predictor variables blood glucose and body mass. This hierarchical structure allowed estimation of both the overall effect across species and the degree of variation among species, while preventing overfitting that would have resulted from modelling species and their interactions with either blood glucose or body mass as fixed effects. Phylogeny was included as a group-level effect using the covariance matrices derived from the ultrametric trees.

To account for the non-linear effects of elevation on species abundance, we fit generalised additive models in mgcv (Wood 2025). To evaluate whether elevation influences the effect of traits on abundance, we included penalized splines for elevation (t2 terms) and their interaction with glucose or body mass. All models accounted for species identity and phylogenetic non-independence. Competing spline formulations were compared, and the selected structures were then fit in 'brms'.

We assessed prior sensitivity by running models with uninformative or weakly informative priors ($\beta \sim N(0, 1)$). Models were run with two Markov chains, each with 10 000 iterations and a 2000-iteration warmup. We evaluated chain convergence using potential scale reduction factors (Gelman and Rubin 1992) and assessed model fit using Bayesian r^2 (Gelman et al. 2019) and posterior predictive checks. For each model, we computed posterior means and 95% credible intervals for the fixed effects (overall trait effects) as well as the estimated variance of the random slopes (species-specific deviations). Model effects were deemed significant if the means and 95% credible intervals did not overlap zero (Lesaffre and Lawson 2012).

In a follow-up analysis, we tested whether body mass varied systematically with elevation (Bergmann 1847, Freeman 2017). We fitted a linear mixed-effects model using the 'lme4' package (Bates et al. 2015) in R. Specifically, we used individual-level body mass measurements as the response variable, with log10-transformed body mass to improve linearity. Species identity was included as a random intercept to account for differences in body mass among species. We first fitted a model including species-specific slopes for elevation. However, since the variance associated with random slopes was negligible ($\sigma = 1.88 \times 10^{-5}$), suggesting little among-species variation in elevational body mass relationships, we simplified the model by retaining only a species-specific random intercept for this analysis.

Results

We found little evidence supporting the abundance-centre hypothesis and, consequently, that abundance distributions are well fitted by symmetric curves (Fig. 1). Conversely, bird species on Mt Cameroon that have broad elevational ranges show varied patterns of abundance distributions. Some species reach their highest abundance at the lower end of their elevational range, others at the upper end, and some somewhere in between (Supporting information). Moreover, only ~20% (10 out of 51) of species had abundance distributions that were best fit by symmetric curves (Fig. 1; Supporting information). Flat abundance distributions (n = 11) were almost equally common as the best fit model, whereas the majority of species' abundance distributions were best fit by the monotonic model (n = 30; Fig. 1). However, four of these species' (*Camaroptera chloronota*, *Illadopsis rufipennis*, *Hedydipna collaris*, and *Macrosphenus concolor*) fitted 'monotonic' curves had a peak abundance near the centre of their elevational range (Supporting information).

Next, we found patterns consistent with the truncated niche scenario. We focused on the shape of both lowland and highland species' abundance distribution. This is because our hypothesis predicts that lowland and highland species exhibit a monotonic abundance increase towards their warm and cold range limit, respectively, such that forest boundaries represent the core of the species' climatic range. Our results revealed that the probability of upper range truncation increased significantly with elevation (p = 0.02; Fig. 2a). Similarly, the probability of lower range truncation increased with decreasing elevation, although the effect was only marginally non-significant (p = 0.06; Fig. 2b). Thus, highland species tend to be more common towards the treeline, whereas lowland species tend to be more common near the lower forest boundary, consistently with the truncated niche scenario.

We tested whether glucose concentrations and body mass influence species' relative abundance. Our results showed no consistent association between physiological traits and the relative abundance of species (Fig. 3). Mean glucose levels did not predict abundance ($\beta = -0.11$; 95% CrI = –1.99, 1.78), although species-specific slopes showed marked heterogeneity ($\sigma = 1.80$; 95% CrI = 0.23, 4.84), suggesting idiosyncratic responses across species (Supporting information). Body mass also did not predict abundance ($\beta = -0.38$; 95%

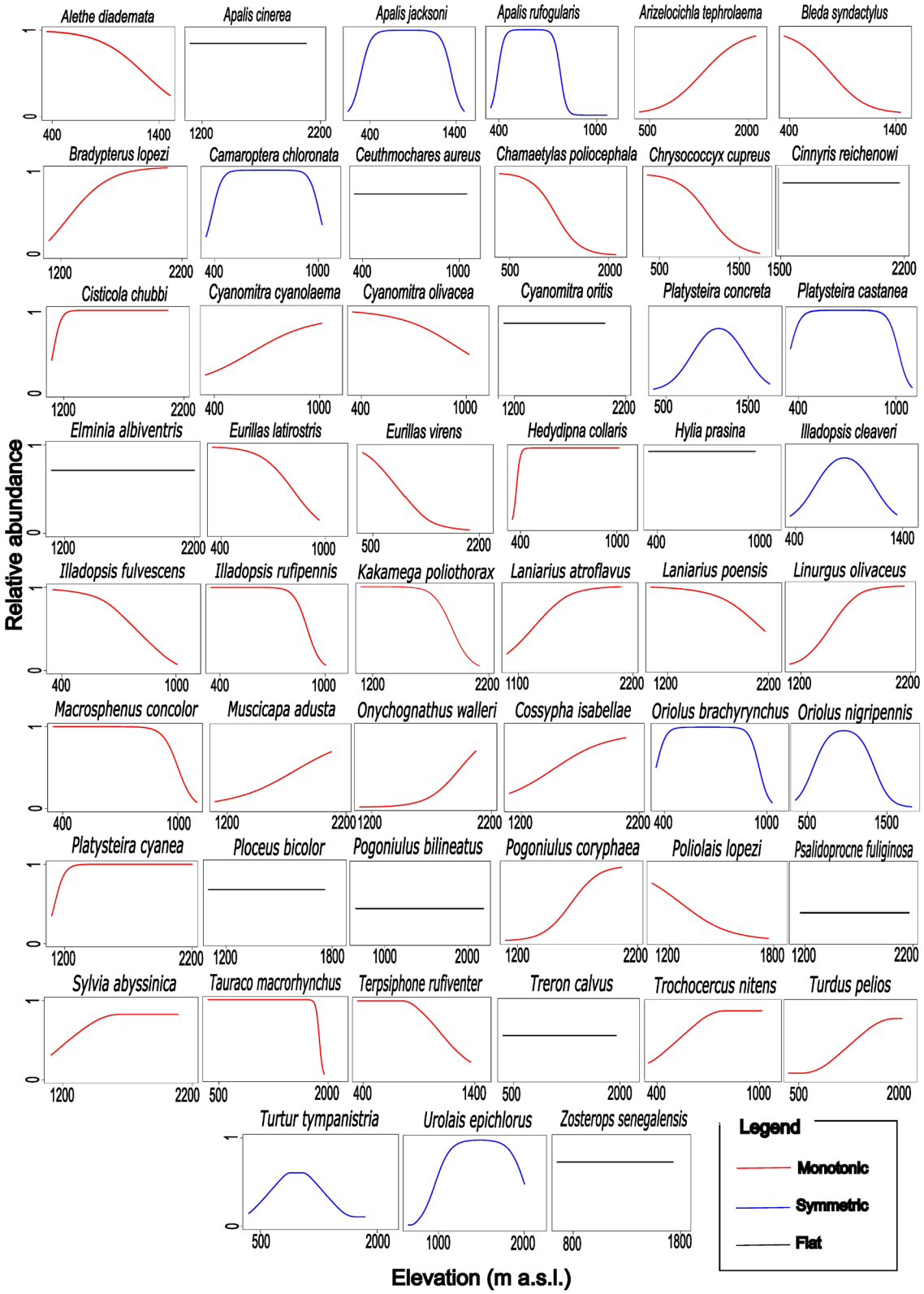

Figure 1. Best fitting Huisman–Olff–Fresco (HOF) model predicting abundance distributions for 51 common species with wide elevational ranges on Mt Cameroon. Line colours represent the best model type for a given species.

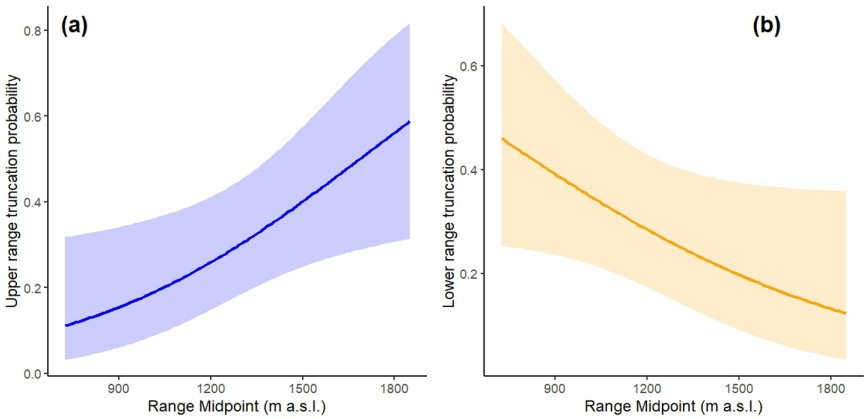

Figure 2. Relationship between elevational range midpoints and the probability of range truncation at upper (a) and lower (b) range limits. Generalized linear models with binomial error distribution show that species with higher elevational range midpoints are more likely to experience upper-range truncation, whereas lowland species tend to show truncation at their lower range limit. Shaded areas represent 95% confidence intervals around the fitted relationships.

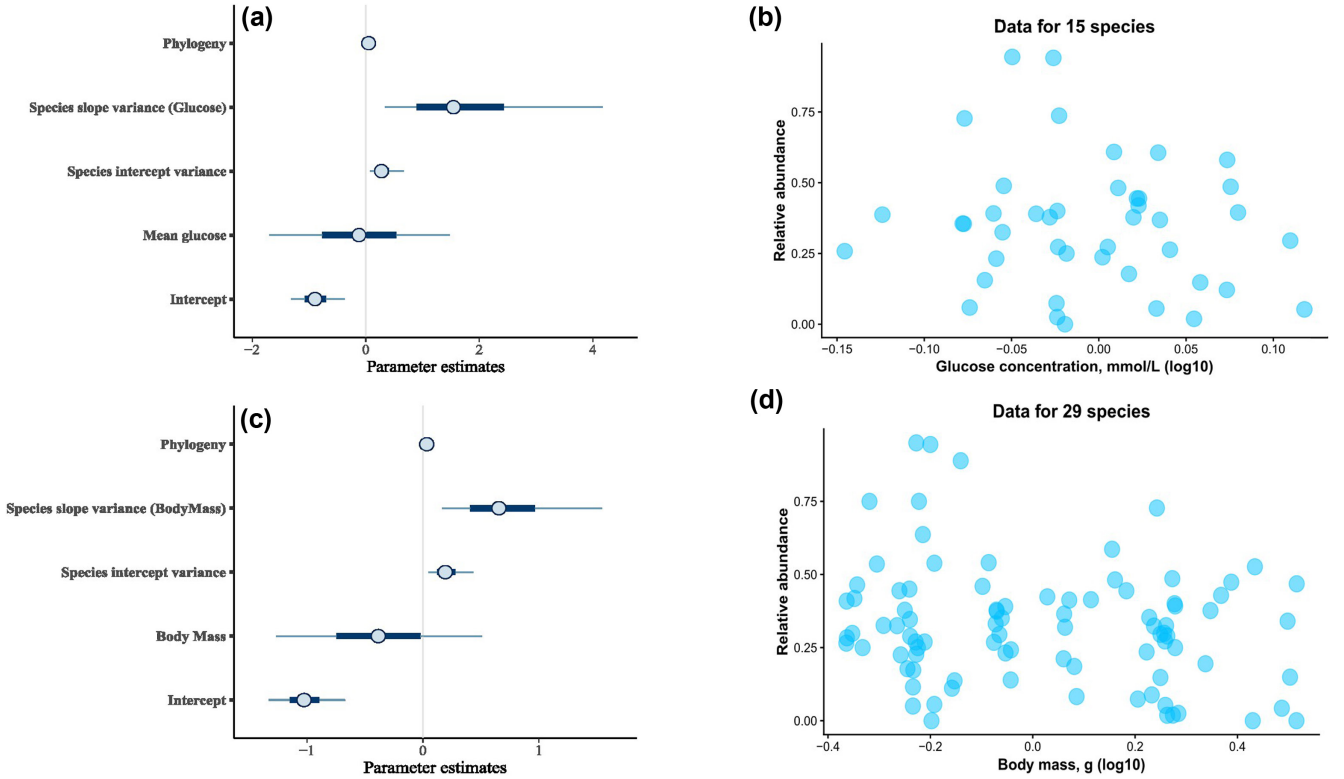

Figure 3. Posterior estimates from Bayesian phylogenetic multilevel models testing the effects of (a) blood glucose concentrations and (c) body mass on species relative abundance. Points represent posterior means; thick and thin horizontal bars indicate 50% and 95% credible intervals, respectively. Panels (a) and (c) show overall parameter estimates, including fixed effects (mean glucose, body mass, intercepts) and variance components (species intercept, slope variance, and phylogeny). Panels (b) and (d) show the relationships between species relative abundance and centred blood glucose concentrations (15 species) and body mass (29 species), respectively.

CrI = –1.43, 0.69), despite moderate interspecific variation in slopes (σ = 0.73; 95% CrI = 0.12, 1.76; Supporting information). Elevation also did not show a significant nonlinear interaction with glucose concentrations and body mass on species abundance (Supporting information). In addition, we found that body mass was not significantly associated with elevation ($F_{1,1500} = 0.26$, p = 0.612; Supporting information).

Discussion

We found little support for the abundance-centre hypothesis in our study of abundance patterns along the elevational gradient of Mt Cameroon. Indeed, while some species are abundant at the centre of their distribution (e.g. *Oriolus nigripennis*, *Platysteira concreta*), the majority deviate from this pattern. Specifically, a large number of species showed the highest relative abundance near their range margins (most of them near the extremes of the forest gradient), whereas only a few exhibited uniform relative abundances across their entire elevational ranges. We also attempted to determine whether life-history traits – blood glucose and body mass – can explain relative abundance patterns. In general, we found no evidence linking glucose concentrations or body mass to abundance, even after controlling for elevation.

Of the 51 species we examined, only 10 (~20%) exhibited the symmetric abundance pattern predicted by the ACH, slightly less than reported in other tropical elevational studies (Freeman and Beehler 2018, Burner et al. 2019). Likewise, a broad review of birds' abundance found that 39% of species conformed to the ACH, slightly higher than our result (Sagarin and Gaines 2002). Weak support for the ACH has also been documented in small mammals. Wen et al. (2021) found that only in almost 9% of the total cases did mammals show a symmetric abundance pattern across several elevational gradients in China. Collectively, our findings and those of these previous studies demonstrate that species generally do not peak in abundance at the centre of their elevational ranges.

The absence of strong support for the ACH could stem from multiple factors. One possibility is that species do exhibit abundant centre patterns, but these are masked by temporal fluctuations in demographic dynamics (Sexton et al. 2009, Freeman et al. 2019). Although the abundance dataset we used was compiled over multiple years rather than through standardized annual surveys across the entire elevational gradient, we suspect that temporal fluctuations did not strongly bias our results. This is because most species in our dataset are invertivores (i.e. invertebrate-eaters), a guild that typically exhibits year-round territorial behaviour and limited elevational migration in the tropics (Diamond 1972, Salisbury et al. 2012, Freeman and Freeman 2014, Barçante et al. 2017). Furthermore, based on our field experience, only a few species in our dataset seem to exhibit regular altitudinal migration (e.g. *Cyanomitra oritis*). Another possibility for the lack of support for the ACH is that interspecific competition could affect species' abundance patterns. For instance, interspecific competition among congeneric species may shape their abundances at sympatric sites (Benítez-López et al. 2014, Wen et al. 2021). This trend implies that sympatric congeners along elevational gradients are expected to exhibit peak abundances at distinct sites within their shared distribution. We found some support for this prediction. For example, *Cyanomitra cyanolaema* was observed to be most common at ~1000 m a.s.l., in contrast to *C. olivacea*, which was more abundant at ~400 m. Similarly, *Laniarius atroflavus* reached peak abundance at higher elevations (2200 m a.s.l.) compared with *L. poensis* (~1000 m). Evidence of interspecific interactions may also emerge from elevational replacements among species (Diamond 1972, Freeman et al. 2022). According to this scenario, the highest abundances of congeners that replace one another along the elevational gradient should occur at their shared range limit. In other words, the tendency of the highest abundance towards the shared range limit between elevational allopatric species should suggest that interspecific competition constrains their distribution. We obtained little support for this prediction, in that we have only one example of elevational replacement between congeners (*Cyanomitra cyanolaema* and *C. oritis*): the lowland *C. cyanolaema* peaks in abundance just below the lower range limit of the highland *C. oritis*, which displays a flat abundance pattern. Our study would have benefited from the inclusion of other elevational gradients across the Cameroon Volcanic Line, where the same congeners of Mt Cameroon occur, to test whether such abundance patterns are due to biotic interactions or abiotic factors (Terborgh and Weske 1975, Wen et al. 2021). Finally, theoretically, the lack of support for the ACH might be linked to human-driven land use changes (Freeman and Beehler 2018). Our data were collected along an elevational gradient of contiguous primary forest, which makes it unlikely that our results are markedly biased by anthropogenic forces. That said, we acknowledge the presence of plantations in proximity to the lower edge of the lowland forest (< 350 m a.s.l.), which may affect species abundances and their distribution. However, if such an effect exists, it would likely appear as reduced abundances of forest species at the lower edge of the forest, potentially biasing our results toward detecting consistently abundant centre patterns in many lowland forest species.

Our logistic model provides strong support for the niche truncation hypothesis (Feeley and Silman 2010, Freeman and Beehler 2018). High-elevation species on Mt Cameroon were more likely to exhibit monotonic increases in abundance with elevation, reaching their highest densities at the upper range limit, which coincides with the treeline. This suggests that while forest-dependent birds may be prevented from expanding beyond the treeline ecotone (Colwell et al. 2004, Jankowski et al. 2010, 2013, Altamirano et al. 2020), they also meet local environmental optima at this boundary. Conversely, lowland species were more likely to show increasing abundances towards their lower elevational range limits, corresponding to the sharp forest edge created by agricultural expansion. In both cases, species abundance patterns reflect truncated realized niches, with environmental or climatic

optima aligning with the elevation of the hard forest boundaries. These results are not particularly striking given that forest boundaries on Mt Cameroon are displaced relative to expected climatic thresholds. Despite the mountain reaching ~4040 m a.s.l., the treeline occurs far below the expected climatic treeline (~3200–3500 m a.s.l.), largely due to periodic volcanic activity, porous substrates, and local hydrological regimes (Doležal et al. 2025, Pernice et al. 2025). At the opposite end of the gradient, oil palm plantations impose an abrupt lower forest edge, which is well above its natural elevation (Hořák et al. 2019). Comparable patterns have been reported elsewhere; for instance, Freeman and Beehler (2018) found that lowland forest species in Papua New Guinea were most abundant near their lower range limits, close to the lowest colonizable elevational zones. Potentially, some species in our study may extend beyond the forest gradient, occurring in montane grasslands within sparse forest patches. Although data on birds' elevational ranges across the full gradient of Mt Cameroon remain scarce (Mlikovsky 2021), forest specialists are rarely observed above the treeline, though Uceda-Gómez et al. (2025) documented *Cinnyris reichenowi* and *Linurgus olivaceus* in treeline grasslands, where they were restricted to small patches of trees and shrubs. This fits their general preference for forest habitat edges and woodlands. Thus, some forest specialists may be capable of occupying higher elevations but appear to be constrained by habitat boundaries. In the absence of such limitations, their distributional patterns might be expected to show greater symmetry. More intensive sampling within montane grasslands could clarify this issue and yield valuable insights into the role of physiographic barriers in shaping species' range limits.

While it has been long recognized that tropical taxa are physiologically specialized to the narrow thermal range typical of their local environments (Janzen 1967, McCain 2009, García-Robledo et al. 2016), we assumed that species' abundance is not directly controlled by abiotic factors (Freeman 2016, Londoño et al. 2017), but rather by other environmental qualities that may regulate population density, such as the local resource availability. However, our analyses showed that the relationship between blood glucose and abundance either within or across species is not significant, thereby rejecting the AGR hypothesis. This finding may reflect several factors. For instance, seasonal fluctuations in blood glucose levels, documented across multiple taxa (Rooke et al. 1986, Schradin et al. 2015), could obscure underlying patterns. However, we controlled for this factor by focusing exclusively on data collected during the dry season. Other diet-related reasons may explain glucose patterns. Our dataset includes mostly invertivores, as mentioned above. Such a bird guild has typically restricted access to dietary sugars and lacks physiological adaptations for efficient carbohydrate digestion (Martínez del Rio 1990). Therefore, invertivores, perhaps, similarly to carnivorous birds, may maintain glucose homeostasis even under prolonged periods of food deprivation through gluconeogenesis, which is supported by a high activity of hepatic enzymes (Migliorini et al. 1973, Veiga et al. 1978, Szarka and Lendvai 2024). If this scenario is accurate, it would hinder the validity of glucose as a proxy for the resource capacity of an environment. Surprisingly, we found no support for the AGR even in frugivores and nectarivores – two guilds that generally show a strong association between food intake and glucose concentrations (Martínez del Rio 1990, Tomášek et al. 2019). In addition, environmental conditions associated with elevation can influence glucose concentrations in birds. Tomášek et al. (2022) have reported that montane birds present higher glucose levels than lowland species. Therefore, we hypothesized that elevation might modify abundance–glucose relationships. However, our models did not predict a strong interactive effect of elevation with glucose on relative abundances for all species examined, perhaps because of the plasticity of this physiological trait (Sweazea et al. 2020). In this case, the adoption of other physiological markers that respond unequivocally to environmental stress (e.g. corticosterone; Hau et al. 2010) may be a valid alternative. Unfortunately, such traits are currently not available for many species in our study. Finally, we do not exclude the possibility that our lack of evidence for the AGR and its interaction with elevation is simply due to our small dataset. Given that, for some species, we were able to sample only a small number of individuals, our estimates of the abundance–glucose relationship may be imprecise. Nevertheless, additional sampling of blood glucose in free-living tropical species will be essential to rigorously evaluate the validity of the AGR. The second physiological trait included in our prediction models was body mass. We found only a weak association between species' body mass and their relative abundance, providing no support for the ABR hypothesis. The ABR hypothesis is based on food limitation. Although we do not have direct measures of food availability, a consistently resource-rich forest gradient could reduce within-species competition for resources, thereby weakening or eliminating any relationship between body mass and abundance. In addition, the relationship between species' abundance and body mass may be influenced by temperature and, consequently, elevation. According to Bergmann (1847), larger body masses are favoured in cooler climates, a pattern supported at the intraspecific level in both mammals (Porter et al. 1994, Steudel et al. 1994) and birds (Ashton 2002). In contrast, we found no evidence that body mass increased with elevation along the Mt Cameroon forest gradient, providing no support for Bergmann's rule in our dataset. Likewise, we found no significant interaction between body mass and elevation on relative abundances. This may be because the upper reaches of Mt Cameroon's relatively short forest gradient do not impose strong thermal stress on local birds. Alternatively, abundant food resources at higher elevations could reduce selective pressure for larger body size, as larger individuals can rely on greater fat stores to endure periods of food scarcity (Boyce 1979, Lindstedt and Boyce 1985).

Conclusion

Our findings reveal that common birds along an Afrotropical elevational gradient do not follow the abundance-centre

hypothesis, instead displaying diverse abundance patterns. Notably, many species are most abundant near their range limits – lowland species near the lower limit and highland species near the upper – often at the edges of the forest gradient. This pattern suggests truncated realized niches and underscores the role of physical habitat barriers in shaping abundance distributions. Furthermore, intrinsic physiological traits such as blood glucose concentration and body mass did not predict species abundances. Future studies incorporating alternative physiological markers of environmental stress could provide a more predictive framework for understanding species abundance along elevational gradients.

Acknowledgement – We are grateful to the local communities of Bokwango and Bakingili villages for their kind and long-term support, and especially to all local guides and students who assisted us during fieldwork. We thank the Mt Cameroon National Park and the Department of Environmental Sciences at the University of Buea, Cameroon, particularly Eric Fokam. This work would not have been possible without the technical support of the Congo Basin Institute in Yaoundé, especially from Kevin Njabo. We also acknowledge Francis Njie Motombi, Francis Luma, Ondřej Sedláček, Kryštof Chmel, and Michal Ferenc for their contributions to the collection of the field data used in this study. This manuscript benefited from insightful discussion with Vojtěch Brlík, which helped to refine its central hypotheses. We would like to thank Elisa Bonaccorso and an anonymous reviewer for their constructive comments.
Funding – Funding was provided by the Czech Science Foundation (project no. 21-17125S and no. 26-22858S).
Conflict of interest – The authors declare no conflict of interest.
Permits – This study was conducted under authorization number 0819PRSB/MINFOF/SETAT/SG/DFAP/SDVEF/SC/ENJ from the Ministry of Forestry and Wildlife of the Republic of Cameroon.

Author contributions

Riccardo Pernice: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Tomáš Albrecht**: Conceptualization (supporting); Formal analysis (supporting); Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (equal). **Oldřich Tomášek**: Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (equal). **Ondřej Kauzál**: Investigation (equal); Writing – review and editing (supporting). **Francis Teke Mani**: Investigation (equal); Writing – review and editing (supporting). **Esembe Jacques Chi**: Investigation (equal); Writing – review and editing (supporting). **Matouš Jančа**: Investigation (equal); Writing – review and editing (equal). **Vincenzo Arizza**: Writing – review and editing (equal). **Daniela Campobello**: Writing – review and editing (equal). **David Hořák**: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/jav.03612.

Data availability statement

Data and code are archived in Dryad Digital Repository: https://doi.org/10.5061/dryad.rn8pk0pqw (Pernice et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Alonso-Alvarez, C. and Ferrer, M. 2001. A biochemical study of fasting, subfeeding, and recovery processes in yellow-legged gulls. – Physiol. Biochem. Zool. 74: 703–713.
Altamirano, T. A., de Zwaan, D. R., Ibarra, J. T., Wilson, S. and Martin, K. 2020. Treeline ecotones shape the distribution of avian species richness and functional diversity in south temperate mountains. – Sci. Rep. 10: 18428.
Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. – Global Ecol. Biogeogr. 11: 505–523.
Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. – Ecol. Model. 157: 101–118.
Barçante, L., Vale, M. M. and Alves, M. A. S. 2017. Altitudinal migration by birds: a review of the literature and a comprehensive list of species. – J. Field Ornithol. 88: 321–335.
Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Grothendieck, G., Green, P. and Bolker, M. B. 2015. Package 'lme4'. – Convergence 12: 2.
Benítez-López, A., Viñuela, J., Suárez, F., Hervás, I. and García, J. T. 2014. Niche-habitat mechanisms and biotic interactions explain the coexistence and abundance of congeneric sandgrouse species. – Oecologia 176: 193–206.
Bergmann, C. 1847. Ober die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. – Gottinger Studien 3: 595–708.
Bibby, C. J., Burgess, N. D., Hillis, D. M., Hill, D. A. and Mustoe, S. 2000. Bird census techniques. – Elsevier.
Blackburn, T. M., Gaston, K. J. and Loder, N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. – Divers. Distrib. 5: 165–174.
Borregaard, M. K. and Rahbek, C. 2010. Causality of the relationship between geographic distribution and species abundance. – Q. Rev. Biol. 85: 3–25.
Boyce, M. S. 1979. Seasonality and patterns of natural selection for life histories. – Am. Nat. 114: 569–583.
Braz, A. G., de Viveiros Grelle, C. E., de Souza Lima Figueiredo, M. and Weber, M. de M. 2020. Interspecific competition constrains local abundance in highly suitable areas. – Ecography 43: 1560–1570.
Breuner, C. W., Delehanty, B. and Boonstra, R. 2013. Evaluating stress in natural populations of vertebrates: total CORT is not good enough. – Funct. Ecol. 27: 24–36.
Brown, J. H. 1984. On the relationship between abundance and distribution of species. – Am. Nat. 124: 255–279.

Brown, J. H., Mehlman, D. W. and Stevens, G. C. 1995. Spatial variation in abundance. – Ecology 76: 2028–2043.
Bürkner, P.-C. 2017. brms: an R package for Bayesian multilevel models using Stan. – J. Stat. Softw. 80: 1–28.
Burner, R. C., Styring, A. R., Rahman, M. A. and Sheldon, F. H. 2019. Occupancy patterns and upper range limits of lowland Bornean birds along an elevational gradient. – J. Biogeogr. 46: 2583–2596.
Burnham, K. P. and Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. – Sociol. Methods Res. 33: 261–304.
Cermeño, P., Marañón, E., Harbour, D. and Harris, R. P. 2006. Invariant scaling of phytoplankton abundance and cell size in contrasting marine environments. – Ecol. Lett. 9: 1210–1215.
Colwell, R. K., Rahbek, C. and Gotelli, N. J. 2004. The mid-domain effect and species richness patterns: what have we learned so far? – Am. Nat. 163: E1–E23.
Damuth, J. 1981. Population density and body size in mammals. – Nature 290: 699–700.
Darwin, C. 1876. On the origin of species by means of natural selection; or, the preservation of favoured races in the struggle for life. – John Murray.
Diamond, J. M. 1972. Avifauna of the Eastern Highlands of New Guinea. – Nuttall Ornithological Club.
Diamond, J. M. 1973. Distributional ecology of New Guinea birds: recent ecological and biogeographical theories can be tested on the bird communities of New Guinea. – Science 179: 759–769.
Doležal, J., Korznikov, K., Bazant, V., Ruka, A. T. and Gago, J. 2025. Elevational shifts in tropical tree leaf traits: interactions between soil, climate, light, and phylogeny. – Plant Ecophysiol. 2: 1.
Feeley, K. J. and Silman, M. R. 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. – Global Change Biol. 16: 1830–1836.
Ferger, S. W., Schleuning, M., Hemp, A., Howell, K. M. and Böhning-Gaese, K. 2014. Food resources and vegetation structure mediate climatic effects on species richness of birds. – Global Ecol. Biogeogr. 23: 541–549.
Fokidis, H. B., Des Roziers, M. B., Sparr, R., Rogowski, C., Sweazea, K. and Deviche, P. 2012. Unpredictable food availability induces metabolic and hormonal changes independent of food intake in a sedentary songbird. – J. Exp. Biol. 215: 2920–2930.
Freeman, B. G. 2016. Thermal tolerances to cold do not predict upper elevational limits in New Guinean montane birds. – Divers. Distrib. 22: 309–317.
Freeman, B. G. 2017. Little evidence for Bergmann's rule body size clines in passerines along tropical elevational gradients. – J. Biogeogr. 44: 502–510.
Freeman, B. G. and Beehler, B. M. 2018. Limited support for the 'abundant centre' hypothesis in birds along a tropical elevational gradient: implications for the fate of lowland tropical species in a warmer future. – J. Biogeogr. 45: 1884–1895.
Freeman, B. and Freeman, A. M. C. 2014. The avifauna of Mt Karimui, Chimbu Province, Papua New Guinea, including evidence for long-term population dynamics in undisturbed tropical forest. – Bull. Br. Ornithol. Club 134: 30–51.
Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M. and Hargreaves, A. L. 2018. Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. – Global Ecol. Biogeogr. 27: 1268–1276.
Freeman, B. G., Tobias, J. A. and Schluter, D. 2019. Behavior influences range limits and patterns of coexistence across an elevational gradient in tropical birds. – Ecography 42: 1832–1840.
Freeman, B. G., Strimas-Mackey, M. and Miller, E. T. 2022. Interspecific competition limits bird species' ranges in tropical mountains. – Science 377: 416–420.
García-Robledo, C., Kuprewicz, E. K., Staines, C. L., Erwin, T. L. and Kress, W. J. 2016. Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. – Proc. Natl Acad. Sci. USA 113: 680–685.
Gaston, K. and Blackburn, T. 2008. Pattern and process in macroecology. – Wiley.
Gaston, K. J. 2003. The structure and dynamics of geographic ranges. – Oxford Univ. Press.
Gelman, A. and Rubin, D. B. 1992. Inference from iterative simulation using multiple sequences. – Stat. Sci. 7: 457–472.
Gelman, A., Goodrich, B., Gabry, J. and Vehtari, A. 2019. R-squared for Bayesian regression models. – Am. Stat. 73: 307–309.
Hau, M., Ricklefs, R. E., Wikelski, M., Lee, K. A. and Brawn, J. D. 2010. Corticosterone, testosterone and life-history strategies of birds. – Proc. R. Soc. B 277: 3203–3212.
Hengeveld, R. and Haeck, J. 1982. The distribution of abundance. I. Measurements. – J. Biogeogr. 9: 303–316.
Hořák, D., Ferenc, M., Sedláček, O., Motombi, F. N., Svoboda, M., Altman, J., Albrecht, T., Djomo Nana, E., Janeček, Š. and Dančák, M. 2019. Forest structure determines spatial changes in avian communities along an elevational gradient in tropical Africa. – J. Biogeogr. 46: 2466–2478.
Hu, Y., Scheffers, B., Pan, X., Hu, H., Zhou, Z., Liang, D., Wenda, C., Wen, Z. and Gibson, L. 2021. Positive abundance–elevational range size relationship weakened from temperate to subtropical ecosystems. – J. Anim. Ecol. 90: 2623–2636.
Hunt, H. L. and Scheibling, R. E. 1998. Effects of whelk (*Nucella lapillus* (L.)) predation on mussel (*Mytilus trossulus* (Gould), *M. edulis* (L.)) assemblages in tidepools and on emergent rock on a wave-exposed rocky shore in Nova Scotia, Canada. – J. Exp. Mar. Biol. Ecol. 226: 87–113.
James, F. C. 1970. Geographic size variation in birds and its relationship to climate. – Ecology 51: 365–390.
Jankowski, J. E., Robinson, S. K. and Levey, D. J. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. – Ecology 91: 1877–1884.
Jankowski, J. E., Merkord, C. L., Rios, W. F., Cabrera, K. G., Revilla, N. S. and Silman, M. R. 2013. The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. – J. Biogeogr. 40: 950–962.
Jansen, F., Oksanen, J. and Jansen, M. F. 2022. Package 'eHOF'. – https://doi.org/10.1111/jvs.12050.
Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – Am. Nat. 101: 233–249.
Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. and Mooers, A. O. 2012. The global diversity of birds in space and time. – Nature 491: 444–448.
Kamga, S. M., Tamungang, S. A., Awa, T., Ewome, F. L., Motombi, F. N., Hořák, D. and Riegert, J. 2022. The importance of forest elephants for vegetation structure modification and its influence on the bird community of a mid-elevation forest on Mount Cameroon, West-Central Africa. – Diversity 14: 227.

Küper, W., Sommer, J. H., Lovett, J. C., Mutke, J., Linder, H. P., Beentje, H. J., Rompaey, R. S. A. R. V., Chatelain, C., Sosef, M. and Barthlott, W. 2004. Africa's hotspots of biodiversity redefined. – Ann. Mo. Bot. Gard. 91: 525–535.
Lack, D. 1947. The significance of clutch-size. – Ibis 89: 302–352.
Larsen, T. S., Lagercrantz, H., Riemersma, R. A. and Blix, A. S. 1985. Seasonal changes in blood lipids, adrenaline, noradrenaline, glucose and insulin in Norwegian reindeer. – Acta Physiol. Scand. 124: 53–59.
Lesaffre, E. and Lawson, A. B. 2012. Bayesian biostatistics. – Wiley.
Lindstedt, S. L. and Boyce, M. S. 1985. Seasonality, fasting endurance, and body size in mammals. – Am. Nat. 125: 873–878.
Londoño, G. A., Chappell, M. A., Jankowski, J. E. and Robinson, S. K. 2017. Do thermoregulatory costs limit altitude distributions of Andean forest birds? – Funct. Ecol. 31: 204–215.
Luiselli, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. – Oikos 114: 193–211.
Maicher, V., Delabye, S., Murkwe, M., Doležal, J., Altman, J., Kobe, I. N., Desmist, J., Fokam, E. B., Pyrcz, T. and Tropek, R. 2020a. Effects of disturbances by forest elephants on diversity of trees and insects in tropical rainforests on Mount Cameroon. – Sci. Rep. 10: 1–11.
Maicher, V., Sáfián, S., Murkwe, M., Delabye, S., Przybyłowicz, Ł., Potocký, P., Kobe, I. N., Janeček, Š., Mertens, J. E. J. and Fokam, E. B. 2020b. Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. – J. Biogeogr. 47: 342–354.
Martínez del Rio, C. 1990. Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. – Physiol. Zool. 63: 987–1011.
Marzoli, A., Piccirillo, E. M., Renne, P. R., Bellieni, G., Iacumin, M., Nyobe, J. B. and Tongwa, A. T. 2000. The Cameroon Volcanic Line revisited: petrogenesis of continental basaltic magmas from lithospheric and asthenospheric mantle sources. – J. Petrol. 41: 87–109.
Mayr, E. 1956. Geographical character gradients and climatic adaptation. – Evolution 10: 105–108.
McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. – Ecol. Lett. 12: 550–560.
McCue, M. D. 2010. Starvation physiology: reviewing the different strategies animals use to survive a common challenge. – Comp. Biochem. Physiol. A Mol. Integr. Physiol. 156: 1–18.
Migliorini, R., Linder, C., Moura, J. and Veiga, J. 1973. Gluconeogenesis in a carnivorous bird (black vulture). – Am. J. Physiol. 225: 1389–1392.
Mlikovsky, J. 2021. Notes on the birds of montane grasslands at Mann's Spring, Mount Cameroon, in the rainy season of 2017. – Malimbus 43: 62–64.
Neate-Clegg, M. H. C. and Tingley, M. W. 2023. Building a mechanistic understanding of climate-driven elevational shifts in birds. – PLoS Clim. 2: e0000174.
Oksanen, J. and Minchin, P. R. 2002. Continuum theory revisited: what shape are species responses along ecological gradients? – Ecol. Model. 157: 119–129.
Paradis, E., Claude, J. and Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. – Bioinformatics 20: 289–290.
Pernice, R., Sedláček, O., Albrecht, T., Tomášek, O., Kauzál, O., Kauzálová, T., Motombi, F. N., Ewome, F. L., Ferenc, M., Chmel, K., Mlíkovský, J., Riegert, J., Kamga, S. M. and Hořák, D. 2025. Functional and phylogenetic structure of forest bird assemblages along an Afrotropical elevational gradient. – Ecol. Evol. 15: e72065.
Pernice, R., Albrecht, T., Tomášek, O., Kauzál, O., Mani, F. T., Chi, E. J., Janča, M., Arizza, V., Campobello, D. and Hořák, D. 2026. Data from: The abundance-centre hypothesis re-examined: body mass, blood glucose, and elevational distributions in Afrotropical forest birds. – Dryad Digital Repository, https://doi.org/10.5061/dryad.rn8pk0pqw.
Porter, W. P., Munger, J. C., Stewart, W. E., Budaraju, S. and Jaeger, J. 1994. Endotherm energetics – from a scalable individual-based model to ecological applications. – Aust. J. Zool. 42: 125–162.
Reif, J., Hořák, D., Sedláček, O., Riegert, J., Pešata, M., Hrázský, Z., Janeček, Š. and Storch, D. 2006. Unusual abundance–range size relationship in an Afromontane bird community: the effect of geographical isolation? – J. Biogeogr. 33: 1959–1968.
Revell, L. J. 2011. phytools: phylogenetic tools for comparative biology (and other things). – Methods Ecol. Evol. 3: 217–223.
Ricklefs, R. E. and Wikelski, M. 2002. The physiology/life-history nexus. – Trends Ecol. Evol. 17: 462–468.
Rimbach, R., Pillay, N. and Schradin, C. 2017. Both thyroid hormone levels and resting metabolic rate decrease in African striped mice when food availability decreases. – J. Exp. Biol. 220: 837–843.
Roberts, W. R., Siepielski, A. M. and Alverson, A. J. 2024. Diatom abundance in the polar oceans is predicted by genome size. – PLoS Biol. 22: e3002733.
Rooke, I. J., Bradshaw, S. D., Langworthy, R. A. and Tom, J. A. 1986. Annual cycle of physiological stress and condition of the silvereye, *Zosterops lateralis* (Aves). – Aust. J. Zool. 34: 493–501.
Sagarin, R. D. and Gaines, S. D. 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? – Ecol. Lett. 5: 137–147.
Sagarin, R. D., Gaines, S. D. and Gaylord, B. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. – Trends Ecol. Evol. 21: 524–530.
Salewski, V. and Watt, C. 2017. Bergmann's rule: a biophysiological rule examined in birds. – Oikos 126: 03698.
Salisbury, C. L., Seddon, N., Cooney, C. R. and Tobias, J. A. 2012. The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. – Ecol. Lett. 15: 847–855.
Sam, K., Koane, B., Bardos, D. C., Jeppy, S. and Novotny, V. 2019. Species richness of birds along a complete rain forest elevational gradient in the tropics: habitat complexity and food resources matter. – J. Biogeogr. 46: 279–290.
Santini, L., Pironon, S., Maiorano, L. and Thuiller, W. 2019. Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. – Ecography 42: 696–705.
Scanes, C. G. and Braun, E. 2013. Avian metabolism: its control and evolution. – Front. Biol. 8: 134–159.
Schradin, C., Pillay, N., Kondratyeva, A., Yuen, C.-H., Schoepf, I. and Krackow, S. 2015. Basal blood glucose concentration in free-living striped mice is influenced by food availability, ambient temperature and social tactic. – Biol. Lett. 11: 20150208.
Sedláček, O., Pernice, R., Ferenc, M., Mudrová, K., Motombi, F. N., Albrecht, T. and Hořák, D. 2023. Abundance variations within feeding guilds reveal ecological mechanisms behind avian species richness pattern along the elevational gradient of Mount Cameroon. – Biotropica 55: 706–718.

Sexton, J. P., McIntyre, P. J., Angert, A. L. and Rice, K. J. 2009. Evolution and ecology of species range limits. – Annu. Rev. Ecol. Evol. Syst. 40: 415–436.
Silva, M. and Downing, J. A. 1995. The allometric scaling of density and body mass: a nonlinear relationship for terrestrial mammals. – Am. Nat. 145: 704–727.
Smith, C. 1950. Seasonal changes in blood sugar, fat body, liver glycogen, and gonads in the common frog, *Rana temporaria*. – J. Exp. Biol. 26: 412–429.
Steudel, K., Porter, W. P. and Sher, D. 1994. The biophysics of Bergmann's rule: a comparison of the effects of pelage and body size variation on metabolic rate. – Can. J. Zool. 72: 70–77.
Sweazea, K. L., Tsosie, K. S., Beckman, E. J., Benham, P. M. and Witt, C. C. 2020. Seasonal and elevational variation in glucose and glycogen in two songbird species. – Comp. Biochem. Physiol. A Mol. Integr. Physiol. 245: 110703.
Szarka, E. Z. and Lendvai, Á. Z. 2024. Trophic guilds differ in blood glucose concentrations: a phylogenetic comparative analysis in birds. – Proc. R. Soc. B 291: 20232655.
Tam, J. C. and Scrosati, R. A. 2011. Mussel and dogwhelk distribution along the north-west Atlantic coast: testing predictions derived from the abundant-centre model. – J. Biogeogr. 38: 1536–1545.
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. and Weske, J. S. 1975. The role of competition in the distribution of Andean birds. – Ecology 56: 562–576.
Tomasek, O., Bobek, L., Kralova, T., Adamkova, M. and Albrecht, T. 2019. Fuel for the pace of life: baseline blood glucose concentration co-evolves with life-history traits in songbirds. – Funct. Ecol. 33: 239–249.
Tomášek, O., Bobek, L., Kauzálová, T., Kauzál, O., Adámková, M., Horák, K., Kumar, S. A., Manialeu, J. P., Munclinger, P., Nana, E. D., Nguelefack, T. B., Sedláček, O. and Albrecht, T. 2022. Latitudinal but not elevational variation in blood glucose level is linked to life history across passerine birds. – Ecol. Lett. 25: 2203–2216.
Uceda-Gómez, G., Molua, L. L., Mani, F. T., Ewome, F. L. and Janeček, Š. 2025. Coping with altitude: altitude-driven floral visitor shifts on *Hypericum revolutum* (Hypericaceae) in Mount Cameroon grasslands. – J. Plant Ecol. 18: rtaf020.
Vágási, C. I., Tóth, Z., Pénzes, J., Pap, P. L., Ouyang, J. Q. and Lendvai, Á. Z. 2020. The relationship between hormones, glucose, and oxidative damage is condition and stress dependent in a free-living passerine bird. – Physiol. Biochem. Zool. 93: 466–476.
Veiga, J. A., Roselino, E. S. and Migliorini, R. H. 1978. Fasting, adrenalectomy, and gluconeogenesis in the chicken and a carnivorous bird. – Am. J. Physiol. Regul. Integr. Comp. Physiol. 234: R115–R121.
Virgós, E., Kowalczyk, R., Trua, A., de Marinis, A., Mangas, J. G., Barea-Azcón, J. M. and Geffen, E. 2011. Body size clines in the European badger and the abundant centre hypothesis. – J. Biogeogr. 38: 1546–1556.
Wen, Z., Cheng, J., Ge, D., Xia, L., Lv, X. and Yang, Q. 2018a. Abundance–occupancy and abundance–body mass relationships of small mammals in a mountainous landscape. – Landsc. Ecol. 33: 1711–1724.
Wen, Z., Wu, Y., Cheng, J., Cai, T., Du, Y., Ge, D., Xia, L. and Yang, Q. 2018b. Abundance of small mammals correlates with their elevational range sizes and elevational distributions in the subtropics. – Ecography 41: 1888–1898.
Wen, Z., Ge, D., Feijó, A., Du, Y., Cheng, J., Sun, J., Wang, Y., Xia, L. and Yang, Q. 2021. Varying support for abundance-centre and congeneric-competition hypotheses along elevational transects of mammals. – J. Biogeogr. 48: 616–627.
White, E. P., Ernest, S. K. M., Kerkhoff, A. J. and Enquist, B. J. 2007. Relationships between body size and abundance in ecology. – Trends Ecol. Evol. 22: 323–330.
Wood, S. 2025. mgcv: mixed GAM computation vehicle with automatic smoothness estimation1.9-3. – https://cran.r-project.org/web/packages/mgcv/.