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Research Article

Species traits mediate the abundant-center patterns in ground-dwelling mammal and bird species in China

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The abundance center hypothesis (ACH) posits that species abundance peaks at distribution centers; however, empirical support remains inconsistent. This study tested the generality of the ACH and investigated species traits as mediators of abundance–distance relationships. We compiled relative abundance indices (RAIs) for 81 ground-dwelling mammal and bird species, comprising 2558 population abundance estimates from standardized camera-trap surveys in China from 2008 to 2023. We assessed correlations between the RAI and population distance to species geographic and climatic centers to evaluate ACH support. We examined phylogenetic signals in the strength of ACH patterns and analyzed the variation in these patterns across taxonomic orders. We also performed formal meta-analyses to estimate mean effect sizes of ACH patterns and examine how species traits mediate the direction and strength of the ACH. We found that only 18% of mammal species and 4% of bird species exhibited significant negative abundance–distance correlations geographically, with similarly limited support climatically (9% mammal species, 12% bird species). Meta-analysis indicated no significant mean effect sizes across species (all $p > 0.05$), contradicting ACH pattern predictions. No phylogenetic signals were observed in abundance–distance relationships. Species exhibiting larger range sizes showed stronger ACH associations. Mammal species exhibiting smaller body sizes and home ranges showed more robust abundance–distance correlations. This study provides limited support for the ACH and suggests it is a context-dependent phenomenon rather than a universal biogeographic rule. Given that species traits mediate ACH strength, conservation strategies should move beyond center-focused approaches to incorporate species-specific abundance patterns.

Keywords: abundance center hypothesis, abundance–distance relationship, climatic niche, geographic distribution, species abundance, species traits

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Introduction

Understanding the relationships between species distribution and abundance is crucial in the fields of macroecology and biogeography (Brown 1984, Sagarin et al. 2006). The abundance center hypothesis (ACH) posits that species abundance peaks at the geographic or environmental center of their distribution (Hengeveld and Haeck 1982, Brown 1984, Sagarin and Gaines 2002). The ACH originated from Grinnell (1922), who analogized the distribution pattern of animal populations to gas molecules dispersing from a central 'metropolis' of high abundance (Sagarin and Gaines 2002). Another explanation is that species range centers consistently exhibit optimal environmental conditions for survival (Brown 1984). Abundance center distribution was historically proposed as a potential 'general rule' of biogeography (Hengeveld and Haeck 1982), and has served as a basis for hypotheses regarding ecological and evolutionary processes (Sagarin and Gaines 2002).

The ACH is highly controversial, with numerous empirical tests both supporting (Fristoe et al. 2023, Martin et al. 2024) and opposing (Tuya et al. 2008, Santini et al. 2019) this hypothesis across various taxonomic groups and ecosystems (Sagarin et al. 2006). A review of 145 individual tests indicated that 61% did not support this hypothesis (Sagarin and Gaines 2002). A large-scale analysis involving more than 1400 species of mammals, birds, fish, and trees revealed that the correlation between species abundance and geographic distance to the distribution center (i.e. the abundance–distance relationship) was non-significant, thereby challenging the general applicability of the ACH (Dallas et al. 2017). Recent studies have extended the testing of the ACH to climatic contexts, suggesting that geographic and environmental niche centers frequently exhibit inconsistencies (Santini et al. 2019, Chevalier et al. 2021). Nevertheless, these studies have yielded mixed results (Martínez-Meyer et al. 2013, Dallas et al. 2017, Osorio-Olvera et al. 2020). The variations in abundance–distance relationships raise questions regarding why certain lineages conform to ACH predictions while others do not.

Life-history traits and ecological strategies of species have been proposed as factors that may moderate abundance–distance relationships. For example, species with higher dispersal capacity, particularly in plants, may enhance conformity to the ACH by improving the tracking of changing environments (Panter et al. 2025). Similarly, adherence to ACH has been observed in North American birds characterized by non-migratory behavior, small body size, narrow niche breadth, and restricted ranges (Osorio-Olvera et al. 2020). However, these patterns are not universal and vary according to taxonomic groups and environmental contexts. For example, larger-bodied mammalian species adhere more strongly to the ACH (Panter et al. 2025), whereas a contrasting pattern is observed in bird species (Osorio-Olvera et al. 2020). In marine ecosystems, species with lower dispersal capacities are more likely to conform to ACH predictions than those with higher dispersal capacities (Ntuli et al. 2020). Overall, the alignment of species abundance distribution with ACH predictions is contingent upon the interactions between life-history traits, dispersal constraints and niche breadth.

The inconsistent results observed in previous studies on the ACH may also stem from methodological biases. Previous studies on ACH testing have frequently employed either absolute abundance (i.e. true population size) or relative abundance as proxy-based metrics (Rivadeneira et al. 2010, Martínez-Meyer et al. 2013, Osorio-Olvera et al. 2020). Ideally, the absolute abundance should be prioritized (Callaghan et al. 2024). However, collecting absolute abundance data is time-consuming, expensive, and often unavailable on a large scale (Callaghan et al. 2024). In contrast, in the absence of standardized protocols, directly comparing raw relative abundance data across independent studies frequently lack spatial comparability due to methodological heterogeneity (Callaghan et al. 2024), and may introduce bias in comparisons between taxa and sites. More importantly, mixing various types of abundance estimate data in testing the ACH may introduce noise and obscure the true abundance–distance relationships (Martínez-Meyer et al. 2013, Santini et al. 2019). Another issue is that temporal mismatches within historical abundance datasets may overlook variations in species abundances over time. These methodological biases can distort interpretations of whether minimal support for the ACH reflects true geographic gradients or false-negative errors. Accurate evaluation of the generality of the ACH necessitates the use of a uniform abundance metric and a spatiotemporally standardized sampling method to minimize methodological effects.

Recent advances in camera-trap technology have greatly improved our ability to collect large-scale species abundance data (Oliver et al. 2023). The non-invasive nature of cameras enables the capture of cryptic and elusive species that are sensitive to human activity (Amir et al. 2022, Hsieh et al. 2024), while also offering a standardized abundance estimate metric that enhances comparability among monitoring sites. In this study, we used camera-trap data of 81 ground-dwelling species (56 mammals and 25 birds) recorded from 2008 to 2023 across China to evaluate the generality of the ACH. We further aim to assess the context-dependency of the ACH and identify the key biological and ecological traits that determine why some species conform to the pattern while others do not. Specifically, we measured the Pearson correlation between species abundance and distance from the distribution center to evaluate the generality of the ACH across 81 ground-dwelling species. Subsequently, we transformed the Pearson correlation coefficients into Fisher's z-scores and tested the phylogenetic signal for the strength of the ACH pattern. Finally, we constructed meta-analytic models to calculate the mean effect size and investigate the impact of biological and ecological traits on abundance–distance relationships. The findings of this study are anticipated to advance our understanding of the ecological and trait-mediated mechanisms shaping species abundance distributions, and provide a theoretical basis for context-specific biogeographic modeling and conservation planning.

Material and methods

Species abundance data

We systematically searched for peer-reviewed studies employing camera-trap technology for wildlife monitoring in China. This search utilized three major Chinese academic databases: the China National Knowledge Infrastructure (www.cnki.net/), Wanfang Data Knowledge Service Platform (www.wanfangdata.com.cn/), and Weipu Chinese Journal database (www.cqvip.com/). We retrieved studies published prior to 31 December 2023, using the following search terms: ('camera trap' OR 'infrared triggered camera' OR 'automatic camera') AND ('wildlife' OR 'mammal' OR 'bird' OR 'vertebrate') AND 'China' in the title field. We restricted our dataset to peer-reviewed studies, thereby excluding gray literature, including dissertations, conference reports, news articles and monographs. We excluded studies employing mixed monitoring methods and those lacking a complete species checklist. We also excluded studies that failed to report population abundance estimates for each species or the technical details used to estimate the population abundance. We excluded studies with fewer than ten infrared cameras or fewer than 180 days and nights (i.e. at least 1800 total camera-trap days) to ensure data quality and comparability. The final dataset comprised 196 publications for downstream analyses (Zhang et al. 2026). The 196 included publications had a median of 60 camera traps (5% and 95% quartiles of 18 and 143 traps), a median survey duration of 455 actual days (5% and 95% quartiles of 210 and 1754 days), and a median of 11889 camera-trap days (5% and 95% quartiles of 2685 and 42 758 camera-trap days).

We extracted geographic coordinates of the reported study ranges and species population abundance estimates from these publications. We standardized the taxonomy in accordance with Wei et al. (2022) for mammals and Zheng (2023) for birds. Notably, some species recently recognized as distinct have historically been classified as subspecies (e.g. takin, Yang et al. 2022, red pandas, Hu et al. 2020). Because the original camera-trap surveys and species range data do not reflect these recent taxonomic splits, we merged recently identified species into previously recognized species groups to reconcile taxonomic differences (Supporting information). The analysis concentrated on ground-dwelling species due to the positioning of camera traps at heights of 0.4–1.0 m above the ground, which restricted the capture of arboreal species. We excluded sambar deer *Rusa unicolor*, Asian small-clawed otters *Aonyx cinerea*, and smooth-coated otters *Lutrogale perspicillata* because of their typical association with wetland habitats and infrequent occurrence in camera-trap surveys. We excluded all rodents except for the Asiatic brush-tailed porcupine *Atherurus macrourus* and Malayan porcupine *Hystrix brachyura* within the order Rodentia. This is because most rodents have small body sizes that complicate their detection and identification in camera-trap photos (Rovero and Zimmermann 2016). We retained only species with more than five population abundance estimates to examine the abundance–distance relationship. The final dataset comprised 56 mammalian species from six orders (i.e. Lagomorpha, Cetartiodactyla, Perissodactyla, Pholidota, Carnivora and Rodentia) and 25 bird species from two orders (Galliformes and Pterocliformes).

Population abundance estimates

We compiled population abundance estimates from the camera-trap studies using the relative abundance index (RAI). Because of inconsistencies in the RAI calculation formulas found in the literature, we standardized the RAI using a method defined as the number of independent valid photos captured of a species per 100 trap days (O'Brien et al. 2003, Palmer et al. 2018):

$$\mathrm{RAI} = \frac{\text{Number of species} - \text{independent valid photos}}{\text{Total camera trap} - \text{days}} \times 100$$

We considered independent detections as those involving different species or belonging to the same species, provided they were separated by a threshold time interval (O'Brien et al. 2003). Most studies have employed independent thresholds of 30 min. The RAI is a detection rate metric that quantifies the frequency of wildlife detections relative to the sampling effort (Sollmann et al. 2013, Chen et al. 2019). It has proven to be linearly correlated with the observed population abundance (Rovero and Marshall 2009, Palmer et al. 2018). More importantly, the RAI is a widely used metric in camera-trap studies across China (Xiao et al. 2022), enhancing the comparability of abundance estimates across various sites.

Geographic and environmental distance

We assessed the abundance–distance relationship by measuring the distance of each population from the species distribution and climatic niche centers. For geographic space analysis, we obtained species range data from the International Union for Conservation of Nature (IUCN) Red List (www.iucnredlist.org) and identified the centroid as the distribution center for each species. We used the Haversine distance to quantify the geographic distance (geoCD) from each population to the species distribution centers (Fig. 1). The climate niche was established by integrating the geographic distribution of the species with climate data. We used 19 bioclimatic variables at a 10 min resolution from the WorldClim ver. 2.0 database (1970–2000 period; Fick and Hijmans 2017). We gridded the geographic ranges of the species at 1° × 1° via ArcGIS 10.8, recorded the species present, and extracted the bioclimatic variables in each grid cell. We performed a principal component analysis (PCA) to establish a two-dimensional global climatic space (Dallas et al. 2017) using R ver. 4.3.3 (www.r-project.org). The first two axes of the PCA explained 75.8% of the variation (Supporting information) and were subsequently used to calculate the environmental distance (envCD) from each population to the climate niche center for each species using Euclidean distance.

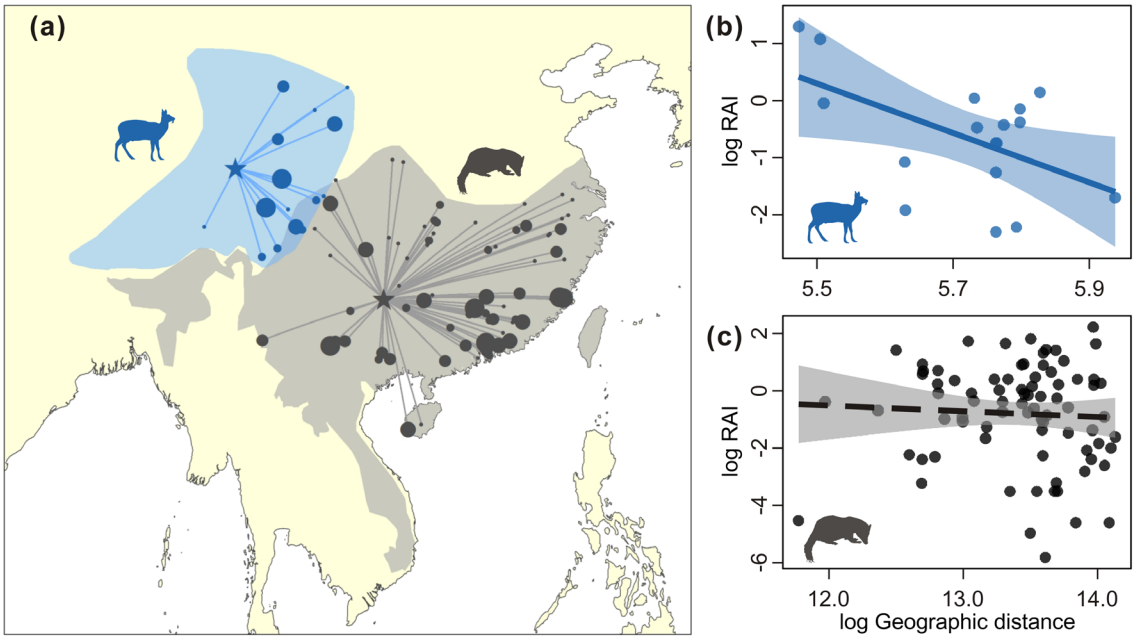

Figure 1. Examples of abundance distribution for the alpine musk deer *Moschus chrysogaster* and the Chinese ferret-badger *Melogale moschata*. The species geographic range are outlined in blue for the alpine musk deer and in gray for the Chinese ferret-badger (a), with centers denoted by pentagrams and sampling points shown as dots, the size of which corresponds to abundance estimates. The scatterplots illustrate the relationships between abundance estimates and distances from each population to the geographic centers for the alpine musk deer (b; follow the abundance-center pattern) and the Chinese ferret-badger (c, deviate from the abundance-center pattern).

Predictor variables

We assembled the biological (body mass and dispersal capacity), ecological (diet diversity, trophic level, habitat breadth and climatic niche breadth), and geographical (range size and centroid latitude) factors that may influence the abundance–distance relationship. Body mass data were sourced from the PHYLACINE ver. 1.2 (Faurby et al. 2018) and AVONET databases (Tobias et al. 2022) for mammals and birds, respectively. We considered the home range as an indicator of the dispersal capacity for mammals (Whitmee and Orme 2013), and hand-wing index (HWI) as an indicator for birds (Sheard et al. 2020). Mammals exhibiting wide home ranges typically utilize more resources and traverse larger areas to meet their energetic demands (Tucker et al. 2014). Birds exhibiting high HWI values demonstrate longer wings and enhanced flight performance, indicating a stronger dispersal capacity (Sheard et al. 2020). We compiled mammalian home range data from Tucker et al. (2014) and bird HWI data from Tobias et al. (2022). The Shannon diversity index was utilized to assess dietary diversity per species based on the dietary proportions from Wilman et al. (2014). The trophic level of mammals was derived from Faurby et al. (2018), which classified each species as carnivores (≥ 70% of food resources from consuming invertebrates or vertebrates), herbivores (≥ 70% of food resources from plants), and omnivores (resources from multiple trophic levels). We omitted trophic-level effects on birds from this analysis because of the omnivorous nature of most Galliformes and Pterocliformes species. Habitat breadth data were obtained from Etard et al. (2020), defined as the number of habitats utilized by a species based on level 2 of the IUCN Habitat Classification Scheme. When the habitat breadth of a species was unavailable (n = 6 species), we employed the mean habitat breadth values at either the genus (n = 4 species) or family (n = 2 species) level as substitutes. Climate niche breadth was calculated using the minimum convex polygon area for each species in the climatic space (Dallas et al. 2017). The range size and centroid latitude of each species were quantified using the counts and median values of 1° × 1° grid cells intersecting with the geographic range of the species. To account for the potential effect of anthropogenic pressure on abundance distributions, we incorporated the human footprint index (HFI) as a predictor variable. We obtained the global HFI data (Mu et al. 2022) and calculated the median HFI value for each species within its geographic range polygon. This metric represents the average level of human pressure across the species' distribution.

Statistical analyses

To account for potential geographical uncertainty in the precise location of populations within reported study areas, we implemented a robust resampling procedure. For each study area, we generated 1000 random points within its spatial boundaries. We then calculated the Pearson correlation coefficients (r) for each species, assessing the relationship between RAI values and distances to species distribution centers (geoCD and envCD) for each of these 1000 points. This process yielded a distribution of 1000 correlation coefficients

per species. We used the median value of these coefficients for each species in all downstream analyses. The geoCD and RAI values were log10 transformed. Negative coefficients were deemed consistent with ACH prediction. We used a meta-analytic approach to synthesize the correlation coefficients across species. We converted the estimated r values into Fisher's Z values (Zr) using Fisher's z transformation: $Zr = 0.5 \times \ln[(1+r) / (1-r)]$ and calculated the variance of the Zr values. We used Zr in a meta-analysis of correlations due to three primary reasons: 1) the sampling distribution of Zr approximates normality, 2) Zr is not constrained between −1 and 1, and 3) the variance of Zr is known and solely dependent on sample size, allowing for robust variance estimation and weighting. Absolute Zr values of 0.1, 0.3, and 0.5 correspond to small, medium, and large effects, respectively (Cohen 1988). Each species-level correlation (Zr) was weighted by the number of population per species (n) to prioritize species with a larger number of population records (Hedges and Olkin 1985): $vi = 1 / (n - 3)$.

We estimated the overall association between RAI value and distance to distribution centers by fitting intercept-only models (i.e. null model) separately for mammals and birds. This approach allowed us to estimate the mean effect size with a 95% confidence interval using the 'rma.mv' function in the R package 'metafor' (Viechtbauer 2010). The effect sizes with 95% confidence intervals overlapping with zero were considered non-significant. We incorporated a phylogenetic correlation matrix generated by the *vcv* function in the R package 'phytools' (Revell 2024) to address autocorrelation between species. We obtained phylogenetic trees from Upham et al. (2019) and Jetz et al. (2012) for mammals and birds, respectively. We utilized a random sample of 100 phylogenetic trees and generated the maximum clade credibility phylogenies using the *maxCladeCred* function in the R package 'phangorn' (Schliep et al. 2017) to account for phylogenetic uncertainty. We calculated the unaccounted heterogeneity (Q) and percentage of variability (I^2) for each model. The I^2 statistic represented the true heterogeneity contributing to the total variation observed across effect sizes, with I^2 values of 25, 50 and 75% indicating low, medium and high heterogeneity, respectively (Higgins et al. 2003).

We assessed the clustering of the strength of the abundance center pattern in phylogeny by quantifying the phylogenetic signal of effect sizes among species. This was accomplished using Blomberg's K (Blomberg et al. 2003) and Pagel's λ (Pagel 1999) via the *phylosig* function in R package 'phytools' (Revell 2024). Values of $K > 1$ signified a strong phylogenetic signal, suggesting that abundance–distance relationships were relatively similar among closely related species. In contrast, $K < 1$ indicated a weaker phylogenetic signal with large differences in the abundance–distance relationships among closely related species. Pagel's λ ranged from 0 to 1: $\lambda = 0$ signified that the abundance–distance relationships were independent of phylogeny (no phylogenetic signal), whereas $\lambda = 1$ indicated a strong phylogenetic signal. In addition, we conducted subgroup meta-analyses at the order level for both mammals and birds to assess variations in effect sizes across different taxonomic orders.

We first performed a Spearman's correlation analysis as a preliminary assessment of the univariate relationships between species traits and Fisher's Z values. To investigate the independent effects of biological (body mass and dispersal capacity), ecological (diet diversity and habitat breadth), and geographical (range size and centroid latitude) factors on abundance–distance relationships, we performed formal analyses using a meta-regression on effect sizes weighted by their variance. The HFI was included as a covariate in the meta-regression models to examine its moderating effect on the abundance–distance relationship. All models were fitted using restricted maximum likelihood through the *rma.mv* function in the R package 'metafor' (Viechtbauer 2010). We conducted separate meta-regressions with each predictor variable treated as a fixed effect, while species and the phylogenetic correlation matrices were incorporated as random effects. We chose a univariate approach rather than a full multivariate model because of the limited sample size of species, particularly for birds ($n = 25$), to ensure model stability and avoid overfitting. Given the high correlations between climate niche breadth and both habitat breadth and range size ($r > 0.7$), we excluded climate niche breadth to avoid collinearity. Body mass, range size, and home range were log10 transformed, and all predictor variables were standardized (mean = 0, SD = 1).

Sensitivity analysis

To test whether our results were robust, we performed sensitivity analyses with zero abundance data and different thresholds of sample size. First, our main analyses excluded all absence records where RAI was equal to zero. However, if the edge 'zeros' are removed, the remaining data (rare but present occurrences) might not show a significant trend. Therefore, we incorporated data from all sampling sites within the compiled studies where a species was surveyed (i.e. camera traps were within the species' distribution) but not detected (RAI = 0) to test for the ACH pattern. To include these zero-abundance values in logarithmic-scale analyses, we transformed the RAI values as $\log10(RAI + 10^{-6})$, where the constant 10^{-6} is an order of magnitude smaller than the minimum non-zero RAI value observed in our dataset. Second, to examine whether the results were sensitive to species with small sample sizes, we repeated the meta-analyses using higher sample size thresholds ($n \geq 10$, 15, 20, and 30 populations per species). This method allowed us to examine whether the overall mean effect size estimates were sensitive to the inclusion of species with small sample sizes.

Results

Generality of the abundance center hypothesis (ACH)

The analysis of the relationship between species abundance and distance from geographic centers revealed mixed results

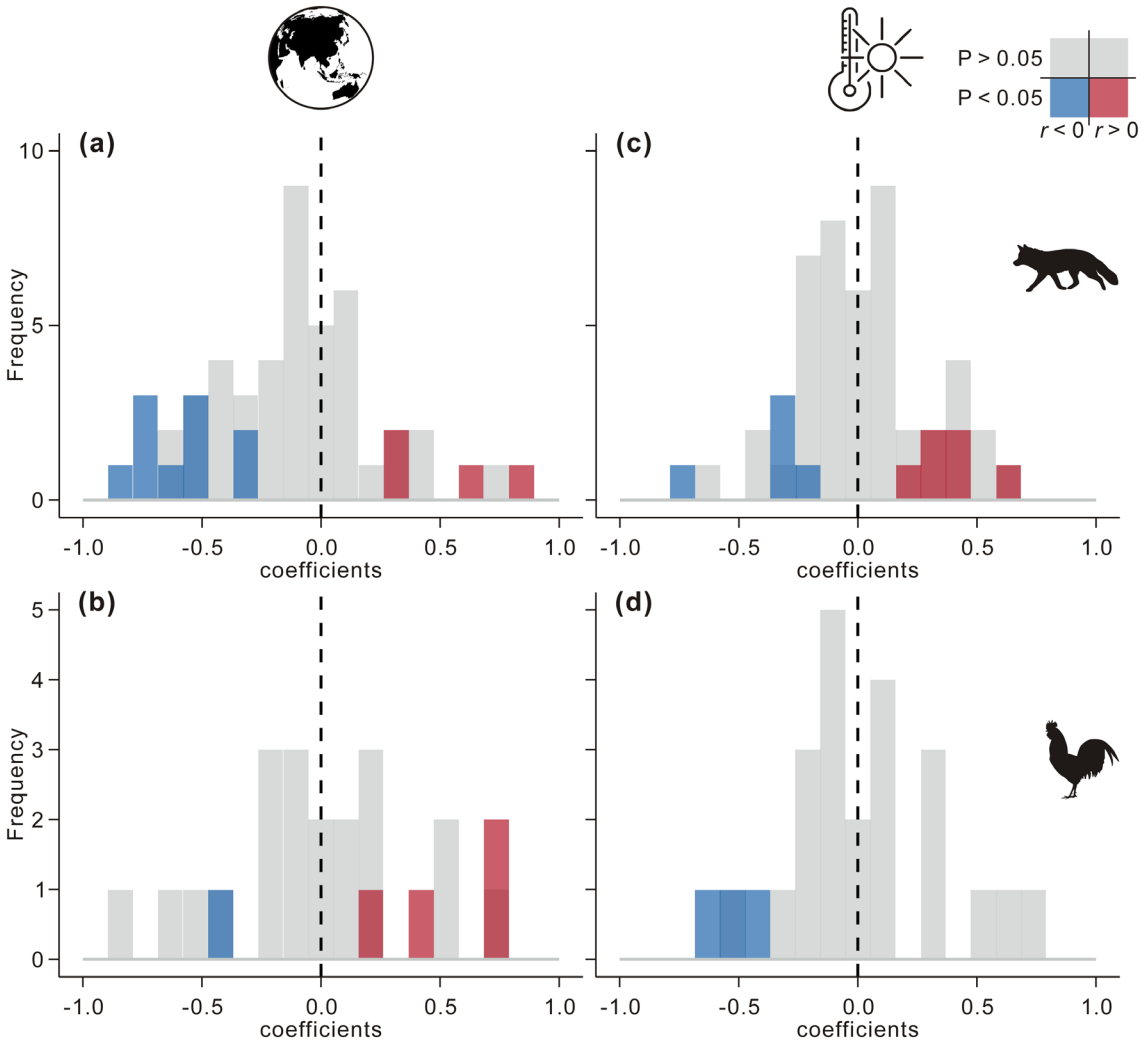

Figure 2. Histograms illustrating the Pearson correlation coefficients of abundance–distance relationships for mammal and bird species in (a)−(b) geographic and (c)−(d) climatic contexts.

for the ACH (Fig. 2a, b). Among all the tested species, 42 of 56 mammal (75%) and 20 of 25 bird (80%) species exhibited no significant geoCD–abundance correlation ($p > 0.05$, Fig. 2a, b, Supporting information). Negative correlations (i.e. consistent with the ACH) were significant in only ten mammal (18%) and one bird (4%) species, whereas four mammal and four bird species showed significant positive correlations (contrary to the hypothesis; Fig. 2a, b, Supporting information). Similarly, 45 mammal (80%) and 22 bird (88%) species exhibited no significant correlation between their abundance and the distance to climate niche centers (Fig. 2c–d, Supporting information). Only five mammal (9%) and three bird (12%) species displayed significant negative envCD–abundance correlations (Fig. 2c, d, Supporting information).

The overall mean effect size estimate for geoCD–abundance correlations was negative for mammal (effect size = −0.073, 95% CI = [−0.373, 0.226]) and bird (effect size = −0.302, 95% CI = [−1.467, 0.862]) species, with neither being significant ($p > 0.05$; Table 1). Alternative estimates of the distance to species distribution centers, measured within climate niches, showed no significant correlations (mammals: effect size = 0.049, 95% CI = [−0.140, 0.238]; birds: effect size = −0.208, 95% CI = [−1.103, 0.688]; both $p > 0.05$; Table 1). Sensitivity analysis, incorporating zero population abundance (RAI = 0) and different sample size thresholds ($n \geq 10$, 15, 20 and 30), yielded results consistent with our primary findings, showing no significant mean effect size for either mammals or birds (Supporting information). Notably, a significant positive correlation was observed between the effect sizes of geoCD–abundance and envCD–abundance relationships (Pearson's $r = 0.25$, $p = 0.027$), indicating that species with higher abundance near their geographic centers also exhibit greater abundance near their climatic centers. The overall effect sizes demonstrated a moderate degree of heterogeneity among mammal ($I^2 = 58.26$ for geoCD and $I^2 = 37.5$ for envCD) and bird ($I^2 = 58.15$ for geoCD and $I^2 = 37.58$ for envCD; Table 1) species as per the criteria established by Higgins et al. (2003), thereby indicating taxonomic variations in abundance–distance relationships.

Table 1. Meta-analytic effect size estimates for abundance–distance correlations in both geographic and climatic contexts for mammals and birds. k = sampling size; CI = confidence interval; p = p values from meta-analytic mixed effects models; I^2 = the true heterogeneity contributing to the total variation observed across effect sizes.

Model	k	Effect size [95% CI]	p	I^2
Geography				
Mammal	56	−0.073 [−0.373; 0.226]	0.632	58.26
Bird	25	−0.302 [−1.467; 0.862]	0.611	58.15
Climate				
Mammal	56	0.049 [−0.140; 0.238]	0.609	37.50
Bird	25	−0.208 [−1.103; 0.688]	0.650	37.58

Phylogenetic signals in abundance–distance relationships

The phylogenetic distribution of abundance–distance relationships indicated considerable variation in the strength of ACH across species (Fig. 3). Both Pagel's λ and Blomberg's K metrics revealed no significant phylogenetic signal for geoCD–abundance effect sizes (mammals: $\lambda = 0$, $p = 1$; $K = 0.108$, $p = 0.269$; birds: $\lambda = 0$, $p = 1$; $K = 0.047$, $p = 0.404$; Supporting information). Similarly, both mammal and bird species exhibited no significant phylogenetic signal for envCD–abundance effect sizes (mammals: $\lambda = 0$, $p = 1$; $K = 0.065$, $p = 0.967$; birds: $\lambda = 0$, $p = 1$; $K = 0.019$, $p = 0.805$; Supporting information). Subgroup-level analyses indicated that neither animal orders exhibited statistically significant abundance–distance relationships (all $p > 0.05$; Supporting information). Moreover, no significant differences in abundance–distance relationships were observed among pairwise comparisons between orders (Supporting information).

Associations between species traits and abundance–distance relationships

Spearman's correlation analysis revealed no significant relationships between species traits and abundance–distance

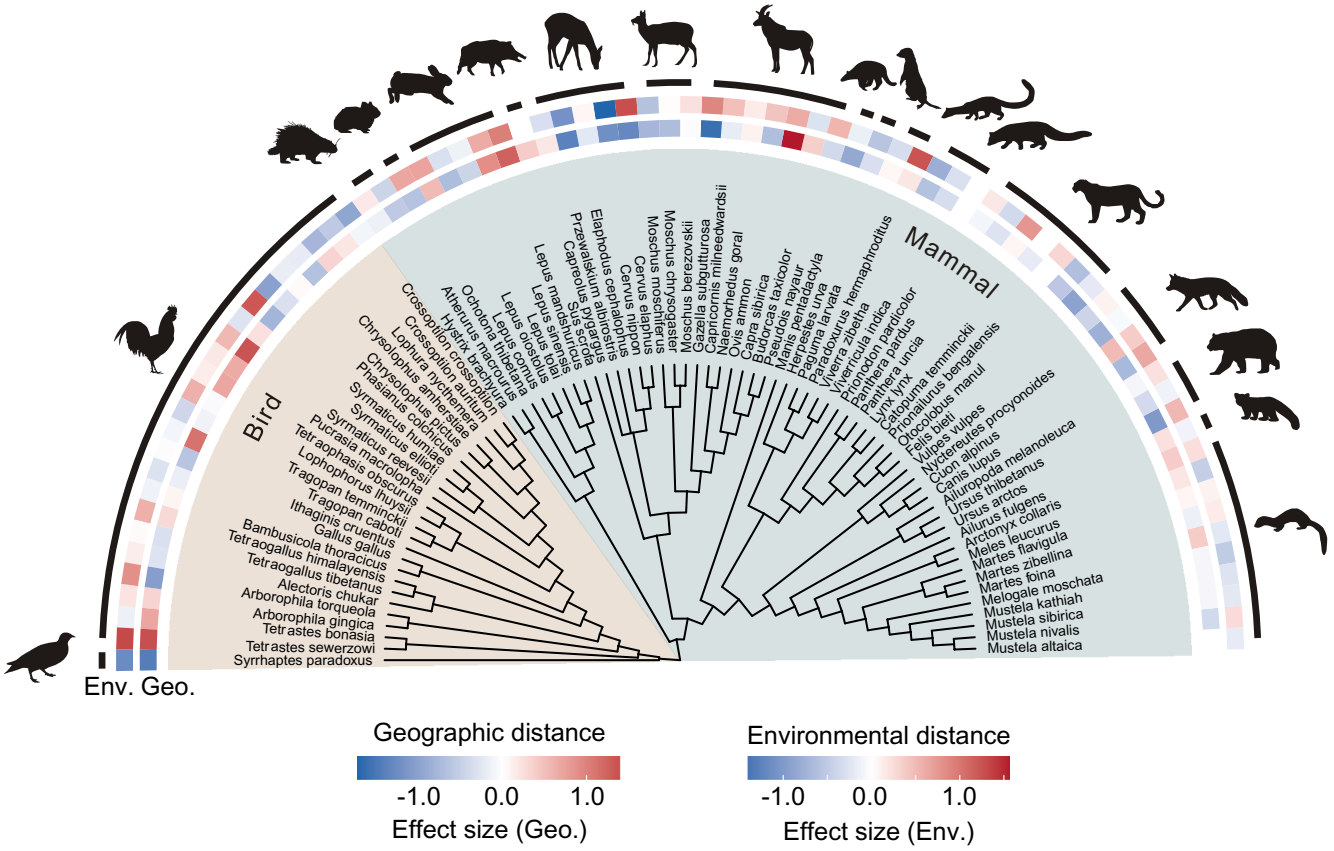

Figure 3. Phylogenetic distribution of effect sizes for abundance–distance correlations across mammal and bird species. The effect sizes are indicated by color gradients, with red indicating a positive effect size and blue signifying a negative effect size. Animal silhouettes representing species within various orders are presented.

correlations in either mammal or bird species ($p > 0.05$; Supporting information). After controlling for phylogenetic relatedness (Fig. 4a, b), the meta-analytic mixed effects models revealed that range size ($\beta = -0.105$, 95% CI = [−0.196, −0.014]) was significantly negatively associated with the geoCD–abundance relationship of mammal species (Fig. 4a, c). This indicates that mammal species exhibiting larger range sizes tend to show stronger adherence to the ACH. None of the bird species traits were significantly associated with the geoCD–abundance relationship (Fig. 4b). Notably, the human pressure was not a significant predictor of whether species follow the ACH measured by geoCD–abundance relationship (Supporting information).

In climatic space, body size ($\beta = 0.071$, 95% CI = [0.001, 0.140]) and home range size ($\beta = 0.091$, 95% CI = [0.012, 0.169]) showed significant positive associations with the envCD–abundance relationship for mammals (Fig. 4a, d, e), indicating that mammal species with larger body size and home ranges were more likely to deviate from the niche center distribution. For bird species, range size ($\beta = -0.181$, 95% CI = [−0.346, −0.016]) was significantly negatively associated with the envCD–abundance relationship (Fig. 4b, f). This suggests that bird species with larger range sizes align more consistently with the ACH in climatic space. We found a negative association between human footprint and deviation from the ACH (Supporting information), implying that species in areas with higher human pressure adhered more closely to the ACH.

Discussion

This study presents an empirical assessment of the ACH based on 2558 population abundance estimates for 81 ground-dwelling species obtained through camera trapping across China. Our multi-taxon analysis revealed that only 13.6% and 9.9% of the species aligned with geoCD–abundance and envCD–abundance correlations, respectively, as predicted by the ACH, thereby indicating limited support for the ACH. The ACH patterns exhibited generally negligible phylogenetic signals, suggesting that phylogenetic constraints have a limited influence in shaping ACH patterns for most species. The adherence of species to the ACH pattern is mediated by species-specific traits, particularly those associated with

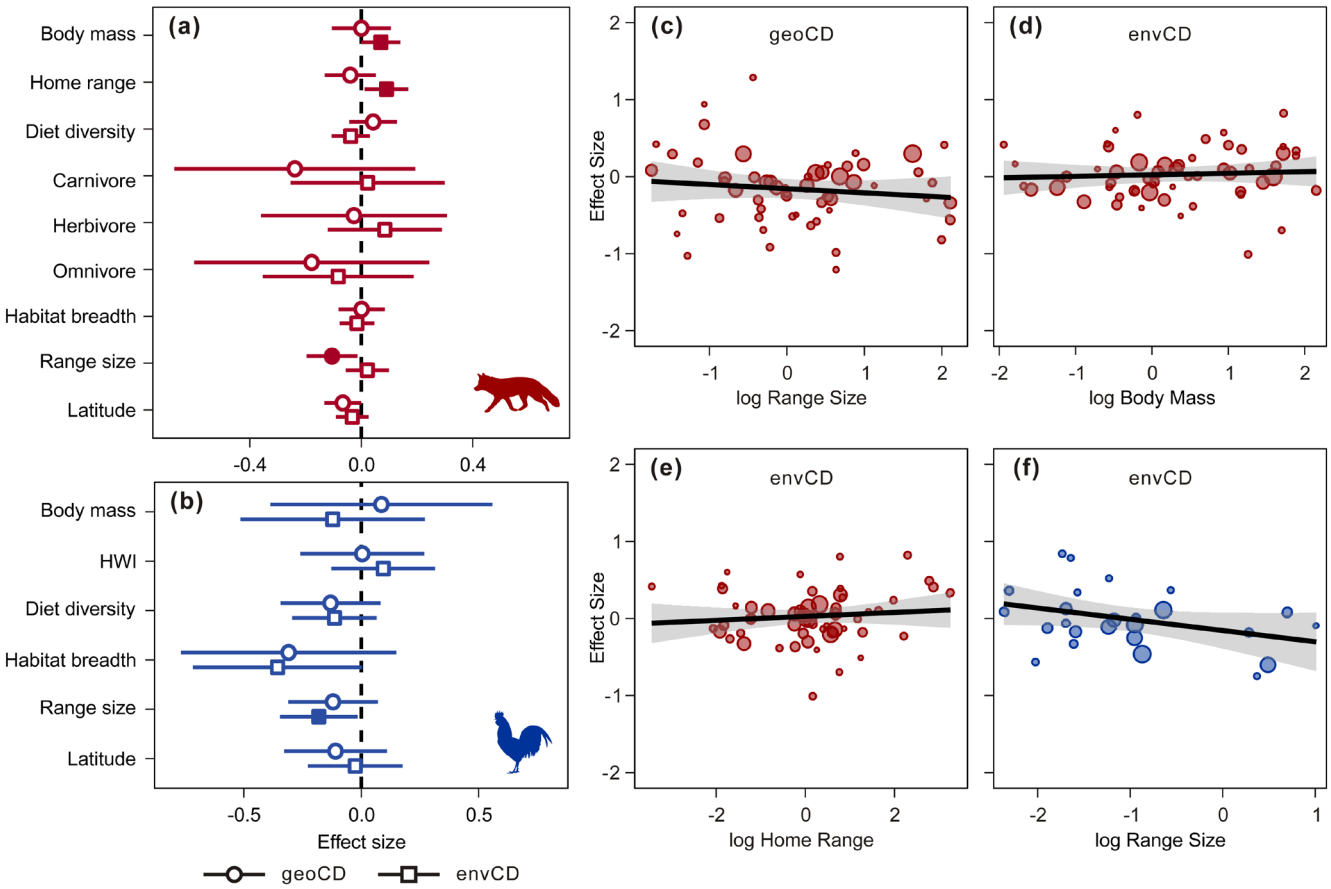

Figure 4. Effect size of species traits on abundance–distance relationships for (a) mammal and (b) bird species. The solid dots indicate significance ($p < 0.05$), while the empty dots denote non significance. The bars represent approximated 95% confidence intervals. Bubble plots illustrate the outcomes of meta-regression analyses examining the effects of moderator variables on the ACH for (c)–(e) mammals and (f) birds. The bubble size is proportional to the sampling size of populations for each species.

species range size, body size and home range. These findings challenge the universality of the ACH and highlight that the decline in abundance at the species distribution edges is taxon- and context-dependent rather than a general biogeographic rule.

Despite using standardized abundance estimates obtained through camera trapping over a limited period (2008–2023), our findings provide mixed evidence for the ACH, thereby supporting a growing body of research challenging the ACH as a biogeographic rule (Sagarin and Gaines 2002, Dallas et al. 2017, Santini et al. 2019, Chevalier et al. 2021). The ideal system of uniform diffusion proposed by Grinnell (1922) does not exist on Earth owing to its complex topography and abrupt climate gradients. In China, high mountain ranges (e.g. the Tibetan Plateau and Hengduan Mountains) and major river systems (e.g. the Yangtze and Yellow Rivers) serve as geographic barriers to species dispersal and create discontinuities in habitat suitability (Cheng et al. 2024). For species limited by these barriers, abundance can peak in the most suitable habitats adjacent to the barriers, as the barriers prevent individuals from dispersing into and establishing populations in areas beyond them. This results in species abundance peaks being located near these geographic barriers rather than at geometric centers (Brown et al. 1996, Dallas et al. 2017). Notably, several species showed significant positive abundance–distance correlations, which contrasts with ACH predictions. In areas characterized by complex topography, geometric mismatches between theoretical range centroids and actual accessible habitats are amplified (Fristoe et al. 2023). For example, the giant panda *Ailuropoda melanoleuca* demonstrates a higher relative abundance and density at the northern edges of its geographical range (e.g. Minshan Mountains in Sichuan Province, China), where food availability, including bamboo density and cover, is greater (Xu et al. 2022). Therefore, it was anticipated that evidence supporting species conformity to the ACH predictions would primarily occur in the plains, with substantially reduced occurrences in mountainous and coastal regions (Fristoe et al. 2023).

In addition to environmental heterogeneity (Dallas et al. 2017), deviations from the ACH pattern may also arise from biotic interactions (Dallas and Hastings 2018, Santini et al. 2019, Wen et al. 2020) and human disturbances (Dallas et al. 2020). The biotic interaction effect was particularly evident in ground-dwelling mammal and bird species because predation and competition frequently occur within these groups. For example, spatial overlap with red foxes *Vulpes vulpes* correlated with considerably lower detection rates of three pheasant species in the Western Sichuan Plateau, thereby highlighting predation pressure on pheasant abundance (Zou et al. 2021). Many studies have documented that anthropogenic activities can disrupt the abundance gradient predicted by the ACH (Freeman and Beehler 2018, Wen et al. 2020). However, our analysis revealed a contrasting pattern where species under higher human pressure tended to adhere more closely to the ACH (Supporting information). This could occur if human-induced range contractions force populations into residual core natural habitats, thus potentially creating a center-peaked abundance distribution in human-modified landscapes. An empirical pattern was observed in the Thai flying fox *Pteropus lylei*, where genetic diversity was greatly correlated with the distribution of Buddhist temples, thereby illustrating the influence of human activity on abundant-center gradients (Chaiyes et al. 2020).

The analysis revealed weak phylogenetic signals in abundance–distance relationships. This finding is similar to that of Dallas et al. (2017), who failed to detect evidence of a phylogenetic signal in the abundance–distance slope for any species group, irrespective of whether distance was measured as geographic distance from the species range centroid or niche distance from the species niche center. In addition, no animal orders showed a significant abundance–distance correlation (Supporting information). These findings suggest that species conformity to the ACH is predicted by species traits and environmental factors rather than by phylogenetic constraints imposed by shared ancestry (Safi and Pettorelli 2010). For most species, adaptive responses to contemporary environmental conditions appear to be more influential than shared evolutionary histories in shaping abundance gradients.

The degree to which a species conforms to the ACH is mediated by its traits, indicating that ACH is a context-dependent phenomenon rather than a biogeographical rule (Chevalier et al. 2021, Panter et al. 2025). The analyses revealed that species with broader ranges showed stronger adherence to the ACH (Fig. 4a, b). In larger species ranges, greater environmental heterogeneity can lead to substantial differences in habitat suitability between the core and peripheral areas. In response, species are likely to concentrate within core areas (Gaston et al. 2000, Panter et al. 2025) or migrate seasonally to access optimal resources and maximize population persistence (Hansen et al. 2010), potentially reinforcing the abundant-center pattern (Baldanzi et al. 2013). In contrast, narrow-ranging species typically inhabit areas characterized by low environmental heterogeneity. The low spatial variations in environmental conditions result in less distinct abundance gradients, thereby rendering ACH consistency inherently weak. Moreover, we observed that mammal species with larger body sizes and home range sizes were less likely to conform to the ACH (Fig. 4d, e). This is attributed to the utilization of large areas by these species for daily activities to locate temporary resources across heterogeneous landscapes; therefore, these species do not concentrate in the central optimal environments. In contrast, small-bodied and narrow-ranging species are more likely to follow the abundance-center pattern owing to their adaptation to stable local environments (Ntuli et al. 2020).

Our findings challenge the generality of the ACH and highlight the need to reevaluate conservation strategies that prioritize species centers. Protecting the core areas of the distribution range and ecological niche remains crucial for numerous species, particularly those with large distribution ranges and strong conformity to ACH patterns. However, our findings indicate that populations at current range margins can maintain a high abundance of many ground-dwelling species

in China. In the context of widespread anthropogenic habitat modification, certain refugee species are now largely confined to such marginal habitats and depend on protected areas for their survival (Kerley et al. 2012, Britnell et al. 2023). This highlights the importance of incorporating contemporary marginal habitats and fragmented habitats into conservation plans (Sexton 2024), particularly in biodiversity-rich areas, such as mountain ranges in China (Xu et al. 2024). In addition, we found that species traits were associated with variation in the strength of the ACH, advocating for species-specific conservation management (Brum et al. 2017). For example, species with larger range sizes were more likely to show adherence to abundance–distance relationships. Large-scale habitat conservation and connectivity management across environmental gradients are essential for these species (Pitman et al. 2017). In contrast, species exhibiting irregular abundance distributions, such as endemic species, may derive greater advantages from targeted conservation efforts within small, protected areas (Volenec and Dobson 2020). Therefore, future strategies should be informed by the actual abundance distribution patterns and specific traits of animals to enhance the effectiveness of conservation efforts and maintain multilevel and multifaceted biodiversity (Devictor et al. 2010).

Several limitations should be acknowledged. First, we used the RAI derived from camera traps, which assumed constant detectability across species and sites. However, detection rates always vary with species-specific life histories and site-specific habitats (MacKenzie et al. 2002, Chen et al. 2019). This variation may cause bias in the abundance estimates for each population, especially concerning rare and social species. Although the majority of surveys in China employ systematic grid designs for biodiversity inventories (Xiao et al. 2022), variations in camera-trap placement strategies (e.g. trail-based versus systematic grids) among studies may introduce bias in detection rates (McShea et al. 2020), potentially influencing the estimated abundance–distance relationships. In addition, while our analysis focused on medium- and large-sized ground-dwelling species to minimize identification errors and used a standardized independence interval, unmeasured variation in detectability remains a source of uncertainty. Finally, camera-trap surveys were predominantly concentrated in the protected areas of forest ecosystems (Meng et al. 2021). This uneven sampling results in spatial bias in eastern and southern China and sampling bias in well-protected habitats with low human disturbance, both of which may decouple species abundance from geographic or climatic gradients. For example, species and populations with core habitats in human-modified landscapes may be oversampled, whereas peripheral populations are likely underrepresented (Sagarin and Gaines 2002, Freeman and Beehler 2018, Santini et al. 2019). Large-scale and well-sampled abundance estimates for terrestrial vertebrates in China is a challenging and ongoing mission (Chi et al. 2020). To the best of our knowledge, this study represents the first effort to utilize camera-trap surveys to assess the generality of the ACH and investigate the factors influencing the abundance–distance relationship. Future studies should examine spatial and temporal discrepancies in the relationship between species abundance and environmental conditions, particularly in the Anthropocene, where human pressures and climate change are disrupting traditional biogeographical patterns.

Conclusions

In summary, this study presents a large-scale assessment of the ACH across 81 ground-dwelling mammal and bird species in China based on standardized abundance estimates derived from camera-trap data. The findings indicate that most species do not exhibit abundance patterns consistent with ACH predictions in either geographic or climatic contexts. The negligible phylogenetic signal in the ACH pattern indicates that evolutionary history has a limited influence in shaping abundance gradients. Instead, species traits, particularly range size, body size, and home range, emerge as key moderators of abundance–distance relationships. These findings suggest that the decline in abundance toward the distribution edge is taxon- and context-dependent rather than a biogeographic rule. This underscores the need to reevaluate conservation strategies that prioritize species centers.

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Author contributions

Ludan Zhang: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Baoming Zhang**: Data curation (equal); Software (equal); Visualization (equal). **Minghui Zhou**: Data curation (equal); Visualization (equal). **Haoting Duan**: Data curation (equal). **Zhipeng Xie**: Data curation (equal). **Xinglin Huo**: Data curation (equal). **Jiehua Yu**: Data curation (equal). **Jiekun He**: Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – review and editing (equal).

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Data availability statement

The data and R code that support the findings of this study are available on Dryad at https://doi.org/10.5061/dryad.51c59zwmp (Zhang et al. 2026).

Supporting information

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

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