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Varying support for abundance-centre and congeneric-competition hypotheses along elevational transects of mammals

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Abstract

Aim: Whether species are most abundant at their geographic range centre and increasingly rare towards range limits (the abundance-centre hypothesis, ACH) has weak empirical support in birds along elevational gradients. This may be due to empirical limitations—most studies do not capture the multi-faceted nature of elevational gradients or species interactions. We examine the ACH and an alternative that the abundance maximum of elevational sympatric congeners will occur at different elevations along a gradient (the congeneric-competition hypothesis, CCH).

Location: Twelve elevational gradients in Central and Southwest China.

Taxon: Five small mammal species, including three congeneric species.

Methods: The ACH was tested by fitting abundance patterns to Huisman-Olff-Fresco (HOF) models and measuring the relative elevational distance between a species' abundance-weighted range centre (RC_{Abu}) and its elevational range centre. The CCH was tested by calculating the elevational overlap value of each congeneric pair and the relative elevational distance ($RC_{AbuDiff}$) between the RC_{Abu}s of congeners.

Results: Abundances of each species showed diverse patterns along different gradients. For all species, a unimodal symmetric pattern appeared at most once among the studied gradients and found in only four (8.7%) of the total cases. Most (90.9%) of the *Apodemus* congeneric pairs had a high elevational overlap (above 75%). For each of the three congeneric pairs, 40.0% to 50.0% of the cases showed $RC_{AbuDiff}$ values > 0.25, suggesting that the congeners' RC_{Abu}s were separated by at least one elevational climate zone.

Main conclusions: Species' elevational abundance patterns may vary among different elevational gradients in the same geographic region. The elevational abundance patterns of five mammalian species were rarely consistent with the ACH after the spatial variability of the patterns was considered. The abundance patterns of congeneric species showed moderate support for the CCH.

KEYWORDS

congeners, elevational gradient, interspecific competition, mountain, scale, spatial replicates, sympatry

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Zhixin Wen and Deyan Ge contributed equally to this work.

1 | INTRODUCTION

Ecologists have long been captivated by the patterns and underlying mechanisms of geographical variation in abundance (Dallas et al., 2017; McGill & Collins, 2003). Across taxa and biomes, one of the fundamental yet controversial rules is the abundance-centre hypothesis (ACH), which predicts that a species is most abundant in the geographical centre of its distribution and becomes increasingly rare towards its range limits (Brown, 1984; Pironon et al., 2017; Sagarin & Gaines, 2002a). Several non-exclusive mechanisms have been proposed to explain the abundant centre distribution. A widely accepted mechanism is that species track the key resources for their survival and breeding, and these resources are assumed to be more abundant and/or of better quality at the centre of the population's range and inferior at the periphery (Virgós et al., 2011). In addition, Brown (1984) argued that local abundance is a reflection of how well a particular site meets the demands of a species along multiple axes (including the species' physiological and ecological characteristics). These characteristics are spatially autocorrelated; thus, sites that are farther from the optimal site (distributional centre) in any direction are less favourable and therefore possess fewer individuals. Given its importance in ecology and relevance to evolutionary (e.g. peripheral populations are more genetically distinct, Sagarin & Gaines, 2002a; Sagarin et al., 2006) and conservation biology (e.g. setting conservation priorities for peripheral populations as they face a higher risk of extinction, Pironon et al., 2017), the ACH has received widespread attention for decades. However, existing empirical evidence is often inconsistent with the ACH, and species abundance distributions show diverse patterns along geographical/environmental gradients. This notion has been explicitly illustrated in meta-analyses (e.g. Sagarin & Gaines, 2002a) and cross-taxon studies (e.g. Dallas et al., 2017; Santini et al., 2019). Considering a wide range of taxa and geographic regions, Sagarin and Gaines (2002a) extracted 145 individual tests from 22 papers and found that only 39% of the tests provided direct support for the ACH.

The observed abundance patterns that are in conflict with the ACH may be driven by various biotic and abiotic factors, such as interspecific interactions (e.g. Abeli et al., 2014—for plants), constrained dispersal (Dallas et al., 2017—for vertebrates and trees), seasonality of local abundance (Santini et al., 2019; Sexton et al., 2009 for birds and mammals) and nonlinear variations in the amount of suitable habitats along the centre-periphery axis (Tam & Scrosati, 2011—for marine invertebrates). In addition, methodological limitations can occur. For example, areas proximate to species range limits are often undersampled compared to range centres, which results in underestimations of abundance at the distribution edge and ultimately an overall biased pattern (Sagarin & Gaines, 2002a). Other methodological limitations may include unstandardized sampling approaches during investigation, failure to cover a species' entire distribution and multidimensional environmental variations due to the polygonal shape of a species' geographic range (reviewed in Santini et al., 2019). Considering both the ecological and methodological complexity of analysing abundance distribution patterns, it remains a challenge to properly test the ACH.

Elevational gradients have been frequently used for testing and developing ecological hypotheses regarding abundance and distribution and their relationship (Brown, 1984; Elsen et al., 2017; Wen, Cheng, et al., 2018). However, several recent studies (only two to our knowledge) have explored the validity of the ACH along elevational gradients, with the elevational abundance patterns of the studied taxa (birds in both studies) showing relatively low support for the hypothesis (Burner et al., 2019; Freeman & Beehler, 2018). Studies along elevational gradients present a number of merits. First, sampling across different elevation sites is easily standardized. Second, environmental variations (e.g. temperature differences) are mostly one-dimensional along elevational gradients, which provides more straightforward insights into the mechanism underlying the abundance pattern (Sagarin & Gaines, 2002b). Third, habitat is relatively continuous along elevational gradients, which minimizes the impact of dispersal limitations (Burner et al., 2019). However, our understanding of the ACH along elevational gradients could be skewed by the fact that much of the evidence so far is drawn from a single animal group. More importantly, these studies have tested the hypothesis along a single gradient and ignored the possible spatial variability in species' elevational abundance patterns. For small mammals, both the abundance and elevational range of the same species could vary among different elevational gradients in the same geographic region (Li et al., 2003; Sánchez-Cordero, 2001). Consequently, the elevational abundance pattern could also vary spatially. Testing the ACH based on empirical evidence from multiple gradients within or among regions is critical for investigating the generality of this assumption.

In addition to abiotic factors and resource availability, species' elevational range limits can be simultaneously determined by interspecific competition. As a result of strong competition, congeneric species that are morphologically and ecologically similar often show abutting or non-overlapping elevational distributions on the same mountain, which has been documented in mammals (Brown, 1971; Kohli et al., 2018; Pasch et al., 2013; Patterson et al., 1998) and birds (Elsen et al., 2017; Freeman, 2015; Terborgh & Weske, 1975). The impact of competition on the range limits of congeneric species has been clearly evidenced by the range expansion of a species in the absence of its congener (e.g. Rickart, 2001). However, some previous studies that reported congeneric species showing parapatric or allopatric elevational distributions also detected sympatric distributions (i.e. having highly overlapping elevational ranges; Elsen et al., 2017; Terborgh, 1971) in a portion of the surveyed taxa. Such sympatry is possibly driven by partitioning of space, time and food resources. For example, two species of coati differentiated in activity times at sympatric elevation sites, which facilitated their coexistence along an Andean elevational gradient (Mena & Yagui, 2019). Nevertheless, the geographic abundance patterns of congeners should, to some extent, be a spatial reflection of competition. Benítez-López et al. (2014) found that the abundance of a sandgrouse species (*Pterocles orientalis*) was negatively affected by the abundance of its congener, *Pterocles alchata*, at sympatric sites. Following the same rationale, it is expected that areas with the abundance maximum of elevational sympatric congeners should be at different elevations of a gradient (the congeneric-competition hypothesis, CCH). This novel hypothesis can be tested along with the ACH by examining congeners' elevational abundance patterns.

In this study, we explored the elevational abundance patterns of five commonly distributed and abundant small mammal species, three of which are congeneric species with highly overlapping elevational ranges, along 12 elevational gradients. Based on the obtained patterns and using these gradients as spatial replicates, we simultaneously tested two hypotheses: (a) species is most abundant at its elevational range centre and becomes increasingly rare towards elevational range limits (Freeman & Beehler, 2018); (b) the abundance maximum of elevational sympatric congeners will occur at different elevations along a gradient.

2 | MATERIALS AND METHODS

2.1 | Study areas

Small mammal abundance data were collected from 12 elevational gradients located in Central and Southwest China, including two in the Qinling Mountain Region (Foping [FP], Pingheliang [PHL]), nine in the Hengduan Mountain Region (Tangjiahe [TJH], Wolong [WL], Jiajin [JJ], Gongga [GG], Emei [EM], Luoji [LJ], CangshanErhai [CSEH], Baima [BM] and Yongde [YD]) and one (Sejila [SJL]) in the Nyainqentanglha Mountain Region (Figure 1). The Qinling Mountain Region, Hengduan Mountain Region and Nyainqentanglha Mountain Region are among the most biologically diverse ecoregions in China because of their high heterogeneity of climates and habitats, extensive elevational ranges, complicated geological structures and unique biogeographic histories (Tang et al., 2006). For small mammals, despite a considerable number of endemic species in each region, some species (e.g. *Niviventer confucianus*, *Sciurotamias davidianus* and *Ochotona thibetana*) are widespread across the regions and occur in most of the elevational gradients previously investigated in the three regions (Wen, Cheng, et al., 2018; Yan et al., 2019).

The 12 elevational gradients were selected because they met the following four criteria: (a) each had at least five elevation sites that were sampled during the field investigation (average: 6.9 ± 1.5 [mean ± *SD*], range: 5–9); (b) the sampling sites spanned an elevational range of more than 1,000 m (average: 2065.7 ± 799.9 m, range: 1,272–4,200 m) that covered most of the elevational range of the mountain slope where the sampling transect was set (see Appendix S1 in Supporting Information, Table S1); (c) the gradients allowed the

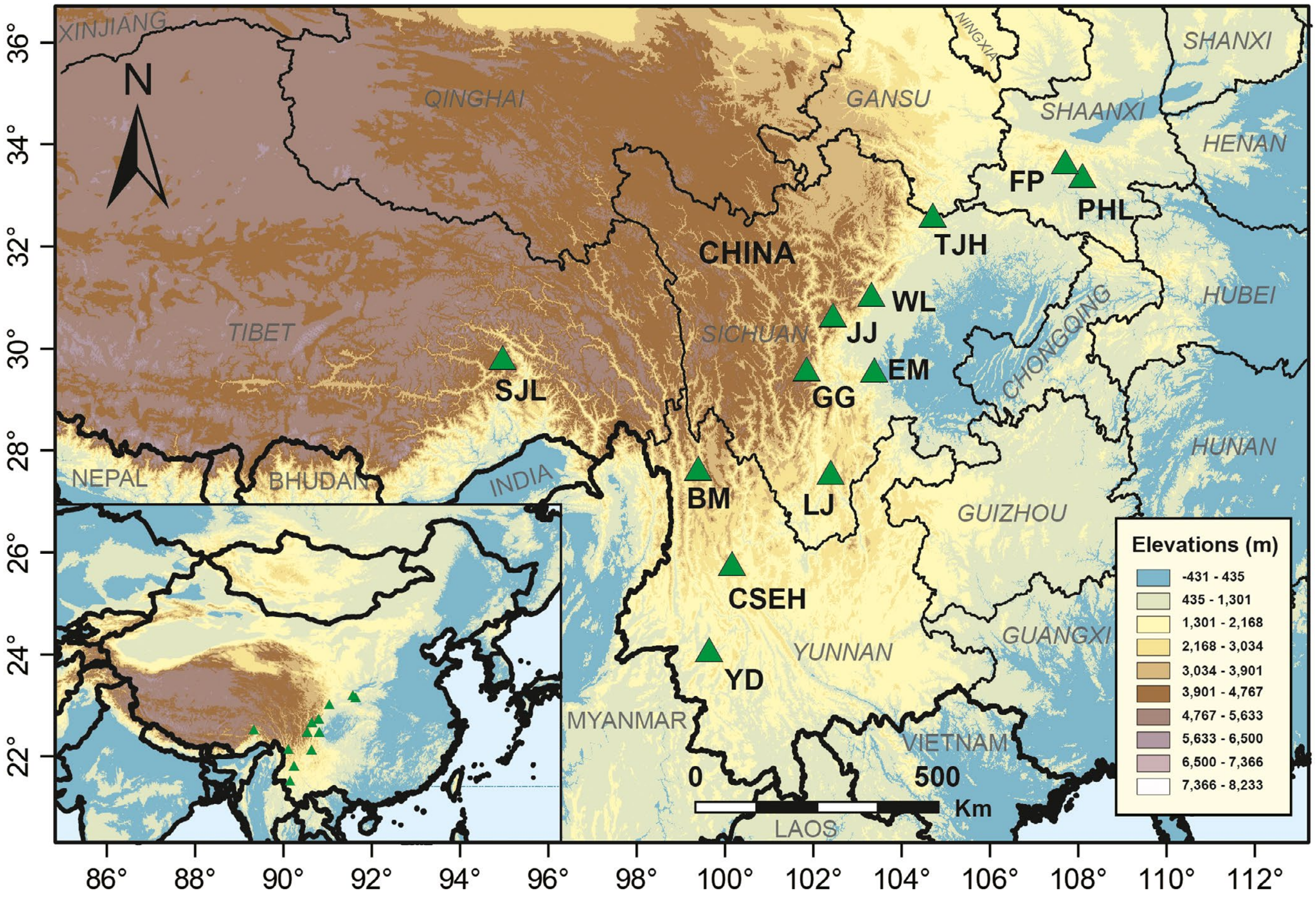

FIGURE 1 Locations of the 12 studied elevational gradients (green triangles) in Central and Southwest China. The Map was projected under the WGS84 system. (Our map did not display area data at a continental, hemispheric, or world scale; and we want to provide the readers the longitude and latitude information of study sites).

investigation to be implemented with a trap-night method, in which more than 1,000 trap-nights (average: 11,382.8 ± 9,023.5, range: 1,248–28,800) were implemented to survey the mammals along the gradient; and (d) both glires (Rodentia and Lagomorpha) and insectivores (Erinaceomorpha and Soricomorpha) could be investigated. Among the gradients, five (GG, BM, SJL, LJ and WL) were surveyed by our group. Each of the sampling sites along the GG gradient ($n = 8$, 1,550–3,500 m) contained 12 standardized trapping quadrats, and each quadrat was made up of 25 snap traps (150 × 80 mm) arranged in a square design (5 × 5) to investigate local small mammal communities. Trapping at each site of GG was conducted in two seasons (early wet season: April to June; late wet season: July to September), and all traps were set for six consecutive nights in each season. At each sampling site along the BM ($n = 6$, 2,500–3,970 m) and SJL ($n = 9$, 2000–4,400 m) gradients, we established six quadrats to trap mammals, with each quadrat encompassing 50 (10 × 5) traps. All sites along these two gradients were surveyed twice over the duration of the study: once in the early wet season and once in the late wet season. The traps were set for five consecutive nights during each season. The LJ gradient was surveyed from April to August 2009. A total of seven sites were surveyed at 400 m-elevation intervals from 1,800 to 4,150 m, and these sites were surveyed only once during the study. Sampling at each site was performed in the same way as that along the Gongga gradient, except the trapping duration was five nights. The WL gradient (eight sampling sites, 1,550–3,500 m) was surveyed on two separate occasions (July–October 2014 and March–June 2015). The taxa at each site were investigated over a three to five-night period on each sampling occasion using 100–240 traps that were arranged into two to five trapping quadrats. For all five gradients, the traps in each quadrat were placed 3–5 m apart and baited with fresh peanuts and dried bean curd. They were set in areas with the most undisturbed habitat at each elevation and covered different microhabitats to record as many species as possible. Small mammal data of the seven other gradients were extracted from the literature (Appendix S1; Tables S2–S13; a list of the data sources is found in Appendix S1).

2.2 | Selected species

To test the spatial variability in the extent to which a species' elevational abundance pattern follows the ACH, we focused on the most commonly distributed and abundant small mammal species across gradients. The selected species should meet the following three criteria: (a) present in more than half of all gradients ($n > 6$); (b) at least 10 individuals have been sampled along each occupied gradient and (c) present in at least three elevation sites along the gradients. These criteria ensured a more rigorous test of the ACH and a sufficient number of gradients to assess spatial variability. Finally, a total of five species satisfied the conditions for use in subsequent analyses: four rodents (*Apodemus chevrieri*, *Apodemus draco*, *Apodemus latronum* and *N. confucianus*) and one shrew (*Anourosorex squamipes*). The number of elevational gradients in which we examined abundance patterns for individual species was as follows: 9 for *A. chevrieri*, 11 for *A. draco*, 8 for *A. latronum*, 11 for *N. confucianus* and 7 for *A. squamipes*. The number of samples along each gradient covered most of the elevational variation of the species selected. The abundance information of each species along each gradient is provided in Appendix S1.

2.3 | Testing the ACH

For each elevation site within a particular gradient, the relative abundance of a species was calculated as its percentage of trap success (the number of individuals captured divided by the number of total trap-nights × 100; Balete et al., 2009; Nor, 2001; Wen, Cheng, et al., 2018). For each species, we used a general linear mixed model (GLMM) to test whether the number of captures (response variable) was correlated with the sampling effort (trap-nights, fixed effect), and elevation, gradient and survey year were included as the random effects. The GLMM was implemented using the R package 'lme4' (*v 1.1-12*; Bates et al., 2016). The results showed that the number of captures was significantly positively correlated with sampling effort for *A. chevrieri* ($Z = 8.488$, $p < 0.001$, $n = 65$), *A. draco* ($Z = 4.061$, $p < 0.001$, $n = 74$), *A. latronum* ($Z = 3.836$, $p < 0.001$, $n = 61$) and *N. confucianus* ($Z = 6.536$, $p < 0.001$, $n = 74$). A significant relationship was only absent for *A. squamipes* ($Z = 1.2$, $p = 0.235$, $n = 48$; Appendix S1; Table S14). Therefore, the percentage of trap success was a robust measure to represent the relative abundance of small mammals and could allow for comparability of the patterns among elevational gradients and taxa in this study.

Then, we fitted the species' elevational abundance pattern to Huisman-Olff-Fresco (HOF) models (*x* axis: elevation; *y* axis: relative abundance) using the R (*v 3.5.1*; R Core Team) package 'eHOF' (*v 1.8*; Jansen & Oksanen, 2013), which allowed for testing of various responses to ecological/environmental gradients. Seven potential HOF distribution models (no response, monotonic, plateau, unimodal symmetric, unimodal skewed, bimodal symmetric and bimodal skewed) were ranked according to their Bayesian information criteria (BIC), with a lower BIC value indicating a better model fit (Raftery, 1995). Following the strategy of Freeman and Beehler (2018), all models with similar likelihoods ($\triangle\text{BIC} \leq 2$ from the top model) were considered to have obtained a good fit. The ACH was considered supported when the distribution followed a unimodal symmetric model (taking into account both the model-fitting results and a visual inspection of the actual elevational abundance pattern). The number of surveyed elevation sites varied from five to nine across the 12 gradients. Usually, it is expected that linear patterns (no response or monotonic) will be favoured with small samples. We therefore built a GLMM to examine whether there was an association between the sample size of the elevation sites and the best-fit abundance distribution. In the model, the best-fit abundance distribution (seven types) was used as the response variable, and number of elevation sites was included as the fixed effect. Species, gradient and survey year were included as random effects.

As the support for the ACH may vary with the spatial scale of analysis (Blackburn et al., 1999; Dallas et al., 2017), we also fitted the species' regional elevational abundance patterns to the HOF models. The abundance and elevation data for the same species were pooled across all elevational gradients (*A. chevrieri*: nine gradients; *A. draco*: eleven gradients; *A. latronum*: eight gradients; *N. confucianus*: eleven gradients; *A. squamipes*: seven gradients) to obtain the regional pattern.

As another prediction of the ACH, the species' elevational range centre (i.e. the midpoint between observed upper and lower range limits) should be highly consistent with the elevation site where the species had the highest relative abundance (i.e. abundance-weighted range centre; Menéndez et al., 2014; Wen, Wu, et al., 2018). To test this prediction, we calculated the species abundance-weighted range centre:

$$\sum_{m.n} E_i * P_{ai}, \tag{1}$$

where *m.n* represent the elevation sites occupied by species *a*, E_i represents the elevation (m) of elevational site *i*, and P_{ai} represents the ratio of individuals of species *a* collected at site *i* to the total number of its individuals collected across the elevational gradient. We then proposed a new metric to measure the relative elevational distance between two types of range centres for individual species:

$$RC_{Diff} = \frac{RC_{Abu} - RC_{Ele}}{ER_{Sp}}, \tag{2}$$

where RC_{Abu} is the abundance-weighted range centre (m), RC_{Ele} is the elevational range centre (m), and ER_{Sp} is the species' elevational range (m). RC_{Diff} ranged from −0.5 to 0.5, where values closer to zero indicated a small difference between RC_{Abu} and RC_{Ele}, a positive value indicated that RC_{Abu} is higher than RC_{Ele}, and a negative value means the opposite. RC_{Diff} was calculated for each species along each gradient. Then, we used Wilcoxon signed-rank tests to assess whether a general trend occurred in the relative elevational positions between the species' RC_{Abu} and RC_{Ele} by pooling data across different gradients. In our dataset, three elevational gradients (JJ, GG and SJL) were sampled with regular sampling intervals (i.e. the elevation intervals between sites were consistent along the whole gradient), while others had irregular intervals. To test whether the species' RC_{Diff} was affected by the irregularity of sampling intervals, we conducted Pearson's correlation analyses between the RC_{Diff} and standard deviation of the sampling intervals of a gradient for each of the five species. The Wilcoxon tests and Pearson's correlation analyses were performed in the R environment.

2.4 | Testing the CCH

The data for three congeneric species (*A. chevrieri*, *A. draco* and *A. latronum*) were used to test the CCH. As a result, a maximum of three congeneric pairs was observed along an elevational gradient. However, due to species absences (certain *Apodemus* species were not caught during investigation) and data deficiency (species with less than 10 individuals) in a given gradient, the number of congeneric pairs for further analyses varied among gradients (1–3, Table 1).

For each congeneric pair along each gradient, we calculated their elevational overlap value as the percentage of the elevational distribution of the smaller-ranged species that overlapped with that of the larger-ranged species. The elevational overlap value varied from 0 (representing a scenario where two species had non-overlapping elevational ranges) to one (the elevational range of the smaller-ranged species was entirely contained within the elevational range of its larger-ranged congener; see Freeman, 2015; Freeman et al., 2019). Pairs that had an elevational overlap value > 0.75 were considered to have elevational ranges that were highly overlapped in this study. Next, we calculated the relative elevational distance between their abundance-weighted range centres as follows:

$$RC_{AbuDiff} = \frac{RC_{mAbu} - RC_{nAbu}}{ER_{Occupy}} \; (RC_{mAbu} > RC_{nAbu}), \tag{3}$$

where RC_{mAbu} and RC_{nAbu} are the abundance-weighted range centres (m) of two congeneric species *m* and *n*, respectively; and ER_{Occupy} is the elevational range (m) of the portion of the elevational gradient that species *m* and *n* occupy. $RC_{AbuDiff}$ ranged from zero, which indicated that both species had the same abundance-weighted range centre, to one, where which indicated that the two points were located at two ends of the portion of the elevational gradient that the two species occupy. Here, we considered $RC_{AbuDiff}$ values > 0.25 to indicate that the CCH was supported by the congeners' elevational abundance patterns. This criterion indicated that even with highly overlapping elevational distributions, their abundance-weighted range centres were at least 300 m (average: 450.8 ± 108.0 m, range: 318.0–700.0 m; $n = 20$) apart and thus separated by one or more elevational climate zones in the mountainous region of Central and Southwest China (Li & Zhang, 2010).

3 | RESULTS

3.1 | ACH

For *A. chevrieri*, the HOF model-fitting results indicated that species abundances showed a unimodal symmetric pattern along two of the nine (22.2%, only the best model was considered) gradients (Figure 2a). Considering the equally well-supported models ($\triangle BIC \le 2$ from the top model), two additional gradients presented species abundance distributions that followed a unimodal symmetric pattern (see Appendix S2 in Supporting Information; Tables S1). However, this pattern was actually found only along the PHL gradient when we plotted species abundance against elevation, and this result was consistent with the ACH. *A. draco* displayed four types of abundance patterns (unimodal symmetric: two gradients [18.2%], other three patterns: nine gradients) along the 11 elevational gradients (Figure 2b). When a visual inspection was performed, the

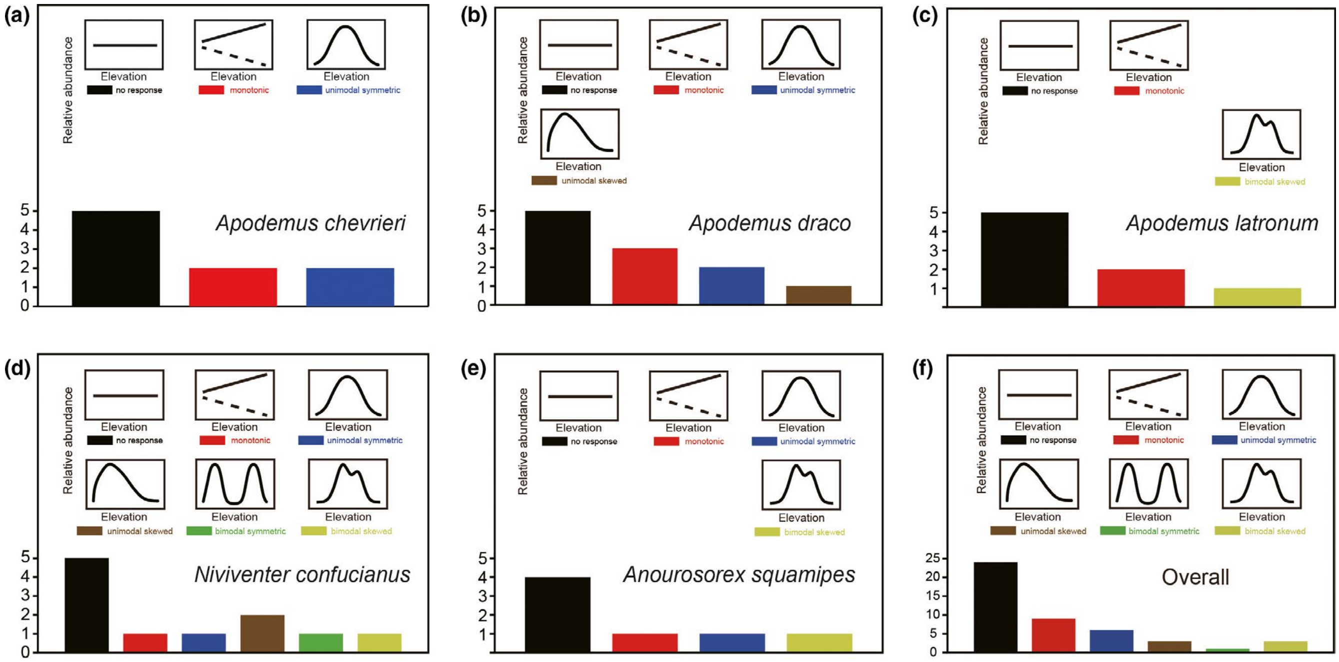

FIGURE 2 Frequencies of each of the six Huisman-Olff-Fresco (HOF) models (no response, monotonic, unimodal symmetric, unimodal skewed, bimodal symmetric, bimodal skewed) in depicting the elevational abundance patterns of (a)*Apodemus chevrieri*(n = 9), (b)*Apodemus draco*(n = 11), (c)*Apodemus latronum*(n = 8), (d)*Niviventer confucianus*(n = 11), (e)*Anourosorex squamipes*(n = 7) and (f) all species combined (n = 46) along the studied gradients. Only the best HOF model (having the lowest BIC value) is considered. A blank spot is shown if the abundance patterns of a species do not fit a particular HOF model

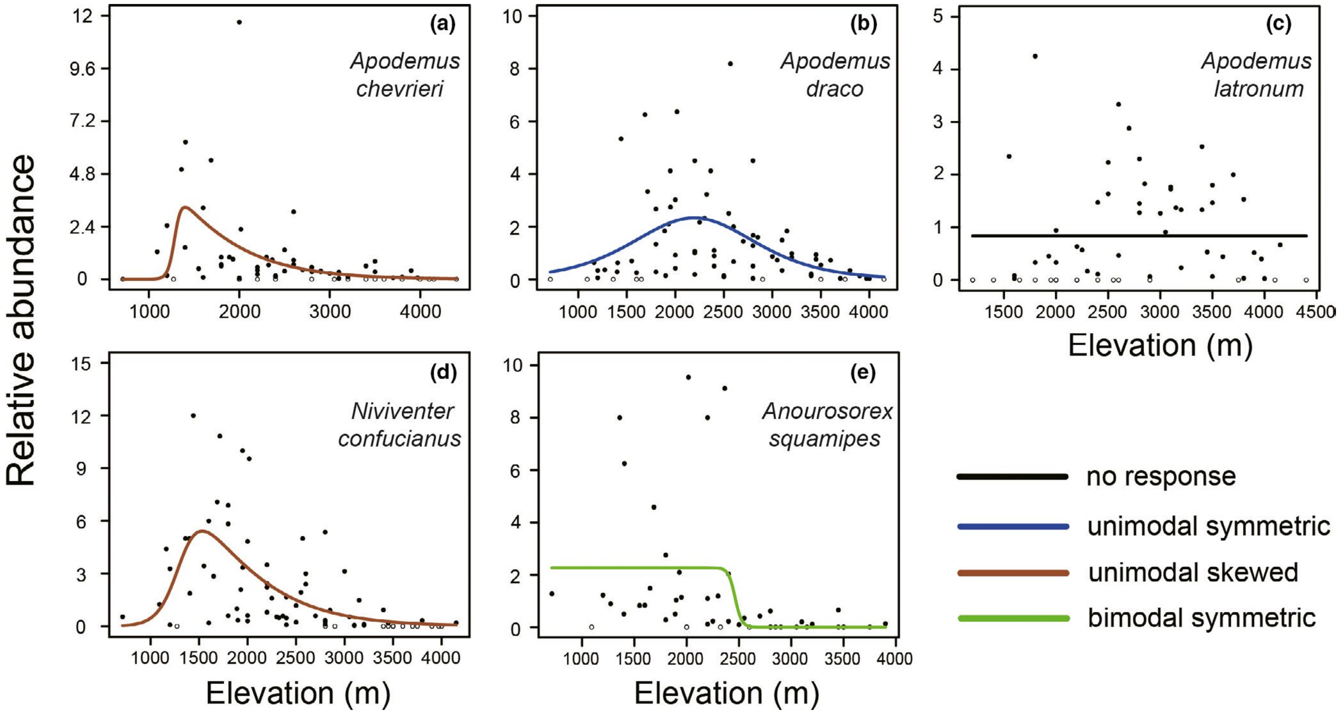

FIGURE 3 Elevational abundance patterns of (a)*Apodemus chevrieri*(n = 65), (b)*Apodemus draco*(n = 74), (c)*Apodemus latronum*(n = 61), (d)*Niviventer confucianus*(n = 74), (e)*Anourosorex squamipes*(n = 48) at the regional scale (xaxis: elevation; y axis: relative abundance). The pattern for each species was obtained by pooling the abundance and elevation data across all elevational gradients (*Apodemus chevrieri*: nine gradients;*Apodemus draco*: eleven gradients;*Apodemus latronum*: eight gradients;*Niviventer confucianus*: eleven gradients;*Anourosorex squamipes*: seven gradients)

species abundance results showed a strict unimodal symmetric distribution only along the YD gradient. For *A. latronum*, three types of distribution patterns were detected and none of the gradients presented a unimodal symmetric pattern (Figure 2c). The elevational abundance pattern of *N. confucianus* showed the most diverse (six) forms (unimodal symmetric: one gradient [LJ, 9.1%]; other patterns: ten gradients) among the five species (Figure 2d). For *A. squamipes*, a unimodal symmetric pattern was observed only along one (WL, 14.3%) of the seven gradients (Figure 2e). The detailed HOF model-fitting results and elevational abundance patterns for each species are provided in Appendix S2 (Tables S2–S47; Figure S1). In summary, a strict unimodal symmetric pattern was found for species' elevational abundance distribution in only four of our cases (8.7%, four of forty-six), suggesting very limited overall support for the ACH. According to the GLMM, the sample size of the elevation sites had little effect on the best-fit abundance distribution across the 12 gradients ($Z = 0.487$, $p = 0.626$; Appendix S2; Table S48).

At the regional scale, the elevational abundance distributions of *A. chevrieri* and *N. confucianus* were best fitted by a unimodal skewed pattern. *A. draco* was the only species for which a unimodal symmetric pattern was observed. No response and bimodal symmetric patterns best described the elevational abundance distributions of *A. latronum* and *A. squamipes*, respectively (Figure 3; Appendix S2; Tables S49–S53).

For both *A. chevrieri* and *N. confucianus*, RC_{Diff} had a constant negative value across gradients (*A. chevrieri*, Wilcoxon signed-rank test: $n = 9$, $Z = -2.67$, $p = 0.008$; *N. confucianus*: $n = 11$, $Z = -2.93$, $p = 0.003$), indicating the species' RC_{Abu}s were located at a lower elevation than their RC_{Ele}s. The same trend was observed in *A. latronum* ($n = 8$, $Z = -2.1$, $p = 0.036$) and *A. squamipes* ($n = 7$, $Z = -2.2$, $p = 0.028$), although a positive RC_{Diff} value was observed in one of the occupied gradients for both species. Only *A. draco* did not show a constant trend in the relative elevational position between RC_{Abu} and RC_{Ele} (positive RC_{Diff}: six gradients, negative RC_{Diff}: five gradients, $Z = -0.267$, $p = 0.79$). The values of RC_{Diff} for the five species increased in the order *A. chevrieri* (−0.207 ± 0.13), *A. squamipes* (−0.178 ± 0.128), *A. latronum* (−0.108 ± 0.102), *N. confucianus* (−0.094 ± 0.025) and *A. draco* (0.005 ± 0.148; Figure 4). In the four cases where species abundances showed a unimodal symmetric distribution, the values of RC_{Diff} were −0.136 (*A. chevrieri* along the PHL gradient), 0.06 (*A. draco* along the YD gradient), −0.063 (*N. confucianus* along the LJ gradient) and −0.15 (*A. squamipes* along the WL gradient). Pearson's correlation analyses demonstrated that RC_{Diff} was only significantly correlated with the standard deviation of the sampling intervals for *A. latronum* ($r = -0.738$, $p = 0.036$). However, these two variables were not correlated for the other four species (*A. chevrieri*: $r = 0.264$, $p = 0.493$; *A. draco*: $r = 0.424$, $p = 0.194$; *N. confucianus*: $r = 0.016$, $p = 0.963$; *A. squamipes*: $r = 0.682$, $p = 0.092$). Overall, the irregularity of the sampling intervals had limited effects on the species' RC_{Diff}. The values of RC_{Abu} and RC_{Ele} of each species are given in Appendix S1 (Tables S2–S13), and the RC_{Diff} values are given in Appendix S2 (Table S1).

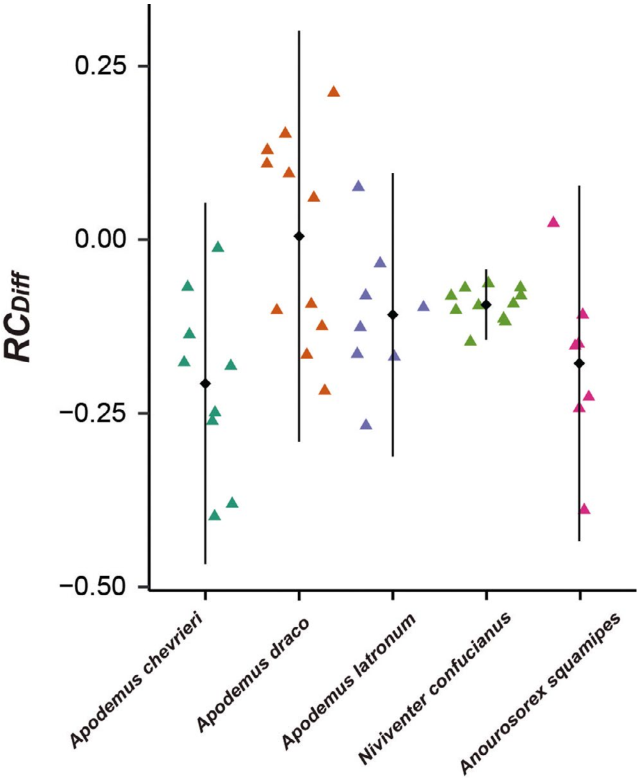

FIGURE 4 Strip charts showing the values of RC_{Diff} (the elevational distance between a species' abundance-weighted range centre and its elevational range centre relative to its elevational range) for each small mammal species across the studied gradients. The numbers of elevational gradients in which we examined abundance patterns for individual species were 9 (*Apodemus chevrieri*), 11 (*Apodemus draco*), 8 (*Apodemus latronum*), 11 (*Niviventer confucianus*) and 7 (*Anourosorex squamipes*). The black diamond and whiskers illustrate the mean and standard deviations of the values of RC_{Diff}, respectively

3.2 | CCH

A total of 22 *Apodemus* congeneric pairs (*chevrieri–draco*: $n = 8$; *draco–latronum*: $n = 7$; *chevrieri–latronum*: $n = 7$) recovered across the 12 elevational gradients. Among them, 20 pairs (90.9%) had an elevational overlap value >0.75; therefore, they were used to test the CCH by calculating their $RC_{AbuDiff}$ values (Table 1). No congeneric pairs showed a constant trend in the relative size of elevational ranges (Wilcoxon signed-rank test, *chevrieri–draco*: $Z = -1.153$, $p = 0.249$; *draco–latronum*: $Z = -1.472$, $p = 0.141$; *chevrieri–latronum*: $Z = 0$, $p = 1$).

A comparison of the elevational positions of RC_{Abu} for each congeneric pair type showed that *A. chevrieri* tended to have a lower RC_{Abu} than both *A. draco* (Wilcoxon signed-rank test: $Z = -2.1$, $p = 0.036$) and *A. latronum* ($Z = -2.366$, $p = 0.018$), while the *draco–latronum* pair showed inconstant trends in the relative position of RC_{Abu} ($Z = -1.014$ $p = 0.31$). The *chevrieri–draco* pair had a $RC_{AbuDiff}$ value > 0.25 along four of the eight (50.0%) gradients. For the *draco–latronum* pair, three gradients had $RC_{AbuDiff}$ values > 0.25 (42.9%). For the *chevrieri–latronum* pair, two of the five gradients (40.0%) showed $RC_{AbuDiff}$

TABLE 1 Elevational overlap value and $RC_{AbuDiff}$ (elevational distance between abundance-weighted range centres of two congeneric species relative to the elevational range of the corresponding elevational gradient) values for each *Apodemus* congeneric pair along 12 gradients. $RC_{AbuDiff}$ values > 0.25 are in bold, suggesting that congeners' abundance-weighted range centres are separated by an elevational distance >300 m and at least one elevational climate zone in the study region

Gradient	*chevrieri---draco*	*draco--latronum*	*chevrieri---latronum*
FP	NA	NA	NA
PHL	1.0/**0.357**	NA	NA
TJH	1.0/**0.335**	1.0/0.186	1.0/0.181
WL	1.0/0.015	1.0/0.072	1.0/0.084
JJ	NA	1.0/**0.262**	NA
GG	1.0/**0.518**	1.0/0.067	0.50/NC
EM	1.0/0.056	NA	NA
LJ	1.0/0.056	0.77/**0.302**	0.52/NC
CSEH	1.0/0.181	1.0/**0.295**	1.0/**0.476**
BM	1.0/**0.287**	1.0/0.005	1.0/**0.283**
YD	NA	NA	NA
SJL	NA	NA	1.0/0.097

Gradient abbreviations: FP: Foping; PHL: Pingheliang; TJH: Tangjiahe; WL: Wolong; JJ: Jiajin; GG: Gongga; EM: Emei; LJ: Luoji; CSEH: CangshanErhai; BM: Baima; YD: Yongde; SJL: Sejila.

NA: not available; NC: not calculated.

values > 0.25 (Table 1). We considered congeners' elevational abundance patterns in these nine cases to be consistent with the predictions of the CCH. Among the three congeneric pairs, *draco–latronum* had a lower $RC_{AbuDiff}$ value (0.170 ± 0.122) than *chevrieri–draco* (0.226 ± 0.178) and *chevrieri–latronum* (0.224 ± 0.162; Figure 5).

4 | DISCUSSION

4.1 | Abundance-centre hypothesis

Our study of species' elevational abundance patterns, including evidence from five commonly distributed and abundant small mammal species along 12 elevational gradients, provides a rigorous assessment of the ACH along the elevational centre-periphery axis, which is largely underrepresented in the ACH literature (Burner et al., 2019). We found very limited evidence supporting the consistent relationship between species abundance distributions and the ACH. Among the five species, *A. draco*, *N. confucianus* and *A. squamipes* occupy a wide range of habitats (e.g. forest, shrubland and farmland) and lifestyles (urban and wildland) in Central and Southwest China while *A. chevrieri* and *A. latronum* are typical forest species that restricted to mountainous areas (Liu & Wu, 2019). However, a unimodal symmetric pattern appeared at most once among the studied gradients for all of them, suggesting the generality of our findings. Weak support for the ACH has also been noted in birds. Freeman and Beehler (2018) found that only one-third of avian species showed a unimodal symmetric abundance distribution along a New Guinean elevational gradient. A similar proportion (30%) of species displayed such spatial patterns on a Bornean mountain (Burner et al., 2019). These previous findings together with our research demonstrate that species may show heterogeneous abundance patterns along an elevational gradient. A typical example is the WL gradient, where four types of abundance patterns were detected for five species. In addition to interspecific variability, our study further indicates that species' elevational abundance patterns vary among different gradients (see the results for *N. confucianus* as a representative species; Figure 2d). Such spatial variability may be due to several factors, including unique biogeographic histories, climatic differences, different levels of interspecific competition within a species' elevational range and demographic stochasticity. It is therefore important to include spatial replicates within or among geographic regions to test for the generality of a species' elevational abundance patterns.

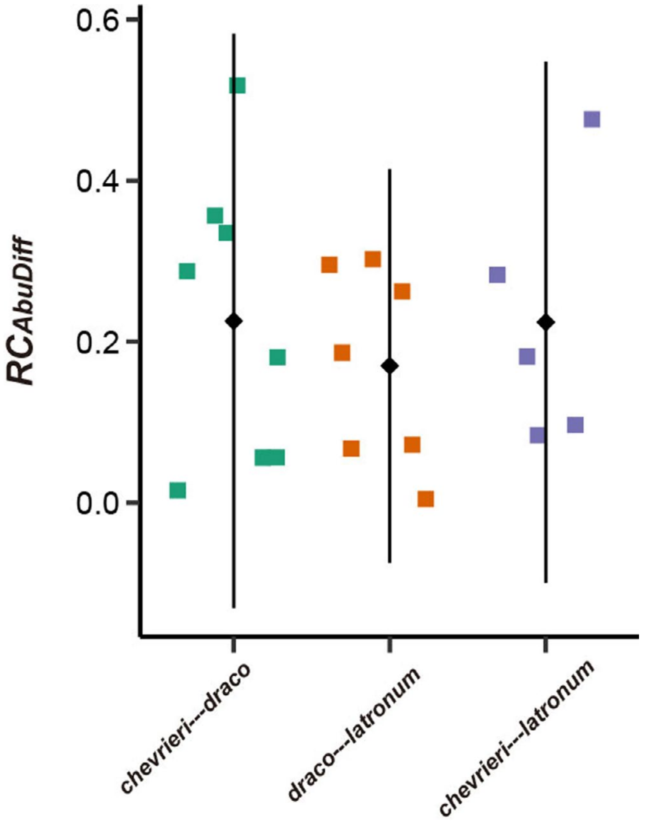

FIGURE 5 Strip charts showing the values of$RC_{AbuDiff}$(the elevational distance between the abundance-weighted range centres of two congeneric species relative to the portion of the elevational gradient that they occupy) for three*Apodemus*congeneric pairs across the gradients. The numbers of gradients in which we calculated the$RC_{AbuDiff}$for each congeneric pair were 8 (*chevrieri–draco*), 7 (*draco–latronum*) and 5 (*chevrieri–latronum*). The black diamond and whiskers illustrate the mean and standard deviations of the values of$RC_{AbuDiff}$, respectively

The lack of support for the ACH could be driven by multiple factors. First, a species' ecological optimum along the gradient may not coincide with its elevational range centre; rather, it may occur anywhere, including the range periphery (Pironon et al., 2017; Wilson et al., 2005). Under the assumption that abundance is higher at sites where the ecological conditions are more favourable, a pattern distinct from that predicted by the ACH may arise (Abeli et al., 2014; Sexton et al., 2009). In our study, four small mammal species showed a consistent trend of $RC_{Abu} < RC_{Ele}$, suggesting that their ecological optima are possibly located at the lower part of the elevational range. The departure of RC_{Abu} from RC_{Ele} was most notable for *A. chevrieri*, which represents a helpful insight for guiding management work and specimen collection of this species (e.g. resulting in a higher potential for capturing more individuals at the lower part of its elevational range with similar efforts). Second, interspecific interactions could have a comparable and even greater effect on species abundance than ecological factors (Brown, 1984; Santini et al., 2019), including along elevational gradients (Ferenc et al., 2016; Wen, Wu, et al., 2018). For example, Ferenc et al. (2016) argued that competitive release caused by a decreasing number of species is responsible for the increasing abundance of avian species at higher elevations because each species can obtain a higher share of environmental resources. Third, temporal variation in local abundance may cause the perceived pattern to be unstable (Freeman et al., 2019; Sexton et al., 2009), and a solution is to conduct a long-term survey to evaluate the temporal consistency of the pattern. Other potential reasons for the weak support for the ACH include human disturbances (e.g. land use change can alter species abundance distributions, Freeman & Beehler, 2018) and the spatial variability of abundance patterns.

Although no response was the dominant pattern when describing the abundance distributions of all five species at the local scale (elevational gradients, Figure 2), different abundance patterns emerged for four species at the regional scale. *A. draco* exhibited a unimodal symmetric pattern, which was consistent with the ACH. From the prospective of elevational abundance patterns, our results reinforced the point that ACH may only be pertinent at certain spatial scales (Pironon et al., 2017; Sagarin et al., 2006). One possible explanation for the disparity between local and regional patterns is that they are governed by different mechanisms. Local climate, interspecific interactions and micro-topographic variations may shape populations and communities of small mammals along a local elevational gradient (Patterson et al., 1989). However, habitat type and biogeographic history may have a stronger effect on the regional pattern (Wen, Cheng, et al., 2018).

4.2 | Congeneric-competition hypothesis

Previous studies have noted that interspecific aggression among congeners is evidence of competition, which in combination with the environment shape the elevational range limits of congeneric pairs (Jankowski et al., 2013). In the present study, we focused on three congeneric small mammal species that are both morphologically and ecologically similar (Li et al., 2012; Wang & Hu, 1999). The results indicated that their elevational ranges substantially overlapped across multiple gradients. Although elevational sympatry instead of parapatry or allopatry for congeneric species has been reported in previous studies on small mammals (McCain, 2004; Rowe et al., 2010) and birds (Elsen et al., 2017), our study presents robust evidence of high spatial overlap. Niche partitioning is a principal mechanism allowing stable coexistence among competing taxa within a local community (Chesson, 2000; Monterroso et al., 2020; Schoener, 1974). Sympatric congeneric species have similar ecological preferences or phenotypes, and they are likely to show differentiation in at least one of the major niche dimensions (e.g. space [habitat], time and food resources) to reduce competition (Andersen et al., 2013; Siemers & Schnitzler, 2004). Niche partitioning may also explain the elevational sympatric distributions of the three *Apodemus* species in our study. At a certain elevation site, species can achieve coexistence by utilizing different volumes of space (e.g. ground vs. tree) or adapting to different food resources. Alternatively, their activities may be separated in time, which was a primary factor underlying the sympatric distributions of two carnivores in northeastern Argentina (Di Bitetti et al., 2009). Li et al. (2012) compared the summer habitats between *A. chevrieri* and *A. draco* in the Tangjiahe Nature Reserve, which is located within the same geographic region as ours, and they found that habitats of the two species were characterized by strong differences in herb height and distance to water resource, which may explain their elevational sympatry in the current study.

Interspecific competition between congeneric species may influence their abundances at sympatric sites, where a negative correlation between abundances often exists (Benítez-López et al., 2014). Following this reasoning, the maximum abundances of elevational sympatric congeners should occur at different sites within their shared range. We obtained some support for this prediction along elevational gradients. For each *Apodemus* congeneric pair type that had a high elevational overlap (above 75%), 40.0% to 50.0% of the cases had $RC_{AbuDiff}$ values > 0.25, indicating that the congeners' RC_{Abu}s were separated by a substantial elevational distance (>300 m). Although such elevational abundance patterns could also be explained by environmental factors (Elsen et al., 2017), such as temperature (e.g. the RC_{Abu} of *A. chevrieri* was consistently lower than that of both *A. draco* and *A. latronum*, which may reflect the former's preference for warmer areas), competition may also play a role here since no inconsistent trend in the relative position of the RC_{Abu} was observed between *A. draco* and *A. latronum* while spatial separation was found along three gradients in which they co-occurred. With spatially separated RC_{Abu}s, elevational sympatric congeners are able to attain greater fitness at the scale of the whole elevational gradient, which may contribute to the high species diversity (encompassing many congeneric species) of montane small mammals in Southwest China from the perspective of coexistence (Du et al., 2017).

5 | CONCLUSIONS

Species' elevational abundance patterns may vary among different elevational gradients in the same geographic region. In our study, the elevational abundance patterns of five mammalian species were rarely consistent with the ACH after the spatial variability of the pattern was considered. However, the abundance patterns of congeneric species showed moderate support for the CCH. Elevational abundance patterns may differ at different spatial scales, thus leading to different degrees of support for the ACH. Our study indicates that spatial replicates (e.g. investigating multiple gradients or performing meta-analysis) can offer opportunities to test for the generality of related patterns and processes. Despite great sampling difficulty, small mammals represent taxa with broad interest in elevational studies worldwide (McCain, 2005) and within specific ecoregions (Wen, Cheng, et al., 2018). Nevertheless, new empirical studies on such species and other vertebrates (e.g. birds and snakes) are still needed for theoretical advances in understanding the patterns of species abundance and distribution and the underlying mechanisms.

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DATA AVAILABILITY STATEMENT

Appendix S1 of Supporting Information provides all the data used in the statistical analysis.

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REFERENCES

Abeli, T., Gentili, R., Mondoni, A., Orsenigo, S., & Rossi, G. (2014). Effects of marginality on plant population performance. *Journal of Biogeography*, *41*(2), 239–249. https://doi.org/10.1111/jbi.12215

Andersen, A. N., Arnan, X., & Sparks, K. (2013). Limited niche differentiation within remarkable co-occurrences of congeneric species: *Monomorium* ants in the Australian seasonal tropics. *Austral Ecology*, *38*(5), 557–567.

Balete, D. S., Heaney, L. R., Veluz, M. J., & Rickart, E. A. (2009). Diversity patterns of small mammals in the Zambales Mts., Luzon, Philippines. *Mammalian Biology*, *74*(6), 456–466. https://doi.org/10.1016/j.mambio.2008.05.006

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Grothendieck, G., & Green, P. (2016). *Package 'Lme4'. Linear mixed-effects models using 'Eigen' and S4*. R package version, 1.1-12. https://cran.r-project.org/web/packages/lme4/index.html

Benítez-López, A., Viñuela, J., Suárez, F., Hervás, I., & García, J. T. (2014). Niche-habitat mechanisms and biotic interactions explain the coexistence and abundance of congeneric sandgrouse species. *Oecologia*, *176*, 193–206. https://doi.org/10.1007/s00442-014-3010-y

Blackburn, T. M., Gaston, K. J., Quinn, R. M., & Gregory, R. D. (1999). Do local abundances of British birds change with proximity to range edge? *Journal of Biogeography*, *26*(3), 493–505. https://doi.org/10.1046/j.1365-2699.1999.00298.x

Brown, J. H. (1971). Mechanisms of competitive exclusion between two species of Chipmunks. *Ecology*, *52*(2), 305–311. https://doi.org/10.2307/1934589

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, *124*(2), 255–279. https://doi.org/10.1086/284267

Burner, R. C., Styring, A. R., Rahman, M. A., & Sheldon, F. H. (2019). Occupancy patterns and upper range limits of lowland Bornean birds along an elevational gradient. *Journal of Biogeography*, *46*(11), 2583–2596. https://doi.org/10.1111/jbi.13691

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology & Systematics*, *31*(1), 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*, *20*(12), 1526–1533. https://doi.org/10.1111/ele.12860

Di Bitetti, M. S., Di Blanco, Y. E., Pereira, J. A., Paviolo, A., & Pérez, I. J. (2009). Time partitioning favors the coexistence of sympatric Crab-Eating Foxes (*Cerdocyon Thous*) and Pampas Foxes (*Lycalopex Gymnocercus*). *Journal of Mammalogy*, *90*(2), 479–490.

Du, Y.-B., Wen, Z.-X., Zhang, J.-L., Lv, X., Cheng, J.-L., Ge, D.-Y., Xia, L., & Yang, Q.-S. (2017). The roles of environment, space, and phylogeny in determining functional dispersion of rodents (Rodentia) in the Hengduan Mountains, China. *Ecology and Evolution*, *7*(24), 10941–10951. https://doi.org/10.1002/ece3.3613

Elsen, P. R., Tingley, M. W., Kalyanaraman, R., Ramesh, K., & Wilcove, D. S. (2017). The role of competition, ecotones, and temperature in the elevational distribution of Himalayan birds. *Ecology*, *98*(2), 337–348. https://doi.org/10.1002/ecy.1669

Ferenc, M., Fjeldså, J., Sedláček, O., Motombi, F. N., Nana, E. D., Mudrová, K., & Hořák, D. (2016). Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: Space limitation in montane forest selects for higher population densities. *Oecologia*, *181*(2), 225–233. https://doi.org/10.1007/s00442-016-3554-0

Freeman, B. G. (2015). Competitive interactions upon secondary contact drive elevational divergence in tropical birds. *The American Naturalist*, *186*(4), 470–479. https://doi.org/10.1086/682703

Freeman, B. G., & 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. *Journal of Biogeography*, *45*(8), 1884–1895. https://doi.org/10.1111/jbi.13370

Freeman, B. G., Tobias, J. A., & Schluter, D. (2019). Behavior influences range limits and patterns of coexistence across an elevational gradient in tropical birds. *Ecography*, *42*(11), 1832–1840. https://doi.org/10.1111/ecog.04606

Jankowski, J. E., Londoño, G. A., Robinson, S. K., & Chappell, M. A. (2013). Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. *Ecography*, *36*(1), 1–12. https://doi.org/10.1111/j.1600-0587.2012.07785.x

Jansen, F., & Oksanen, J. (2013). How to model species responses along ecological gradients - Huisman-Olff-Fresco models revisited. *Journal of Vegetation Science*, *24*(6), 1108–1117. https://doi.org/10.1111/jvs.12050

Kohli, B. A., Terry, R. C., & Rowe, R. J. (2018). A trait-based framework for discerning drivers of species co-occurrence across heterogeneous landscapes. *Ecography*, *41*(12), 1921–1933. https://doi.org/10.1111/ecog.03747

Li, J.-S., Song, Y.-L., & Zeng, Z.-G. (2003). Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecology and Biogeography*, *12*(6), 449–460. https://doi.org/10.1046/j.1466-822X.2003.00052.x

Li, W.-H., & Zhang, Y.-G. (2010). *Vertical climate of Hengduan Mountains and the impact on forest distribution*. China Meteorological Press. (In Chinese).

Li, Y.-X., Zhang, Z.-J., Sun, Y.-R., Chen, L.-M., Yang, X.-G., & Hu, J.-C. (2012). A comparison of summer habitats selected by sympatric *Apodemus chevrieri* and *Apodemus draco* in Tiangjiahe Nature Reserve. *China. Acta Ecologica Sinica*, *32*(4), 1241–1248 (In Chinese).

Liu, S.-Y., & Wu, Y. (2019). *Handbook of the mammals of China*. The Straits Publishing & Distribution Group. (In Chinese).

McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *Journal of Biogeography*, *31*(1), 19–31. https://doi.org/10.1046/j.0305-0270.2003.00992.x

McCain, C. M. (2005). Elevational gradients in diversity of small mammals. *Ecology*, *86*(2), 366–372. https://doi.org/10.1890/03-3147

McGill, B., & Collins, C. (2003). A unified theory for macroecology based on spatial patterns of abundance. *Evolutionary Ecology Research*, *5*(4), 469–492.

Mena, J.-L., & Yagui, H. (2019). Coexistence and habitat use of the South American coati and the mountain coati along an elevational gradient. *Mammalian Biology*, *98*(2), 119–127. https://doi.org/10.1016/j.mambio.2019.09.004

Menéndez, R., González-Megías, A., Jay-Robert, P., & Marquéz-Ferrando, R. (2014). Climate change and elevational range shifts: Evidence from dung beetles in two European mountain ranges. *Global Ecology and Biogeography*, *23*(6), 646–657. https://doi.org/10.1111/geb.12142

Monterroso, P., Díaz-Ruiz, F., Lukacs, P. M., Alves, P. C., & Ferreras, P. (2020). Ecological traits and the spatial structure of competitive coexistence among carnivores. *Ecology*, *101*(8), e03059. https://doi.org/10.1002/ecy.3059

Nor, S. M. (2001). Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography*, *10*(1), 41–62. https://doi.org/10.1046/j.1466-822x.2001.00231.x

Pasch, B., Bolker, B. M., & Phelps, S. M. (2013). Interspecific dominance via vocal interactions mediates altitudinal zonation in Neotropical singing mice. *The American Naturalist*, *182*(5), E161–E173. https://doi.org/10.1086/673263

Patterson, B. D., Meserve, P. L., & Lang, B. K. (1989). Distribution and abundance of small mammals along an elevational transect in temperate rainforest of Chile. *Journal of Mammalogy*, *90*(1), 67–78.

Patterson, B. D., Stotz, D. F., Solari, S., Fitzpatrick, J. W., & Pacheco, V. (1998). Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography*, *25*(3), 593–607. https://doi.org/10.1046/j.1365-2699.1998.2530593.x

Pironon, S., Papuga, G., Villellas, J., Angert, A. L., García, M. B., & Thompson, J. D. (2017). Geographic variation in genetic and demographic performance: New insights from an old biogeographical paradigm. *Biological Reviews*, *92*(4), 1877–1909. https://doi.org/10.1111/brv.12313

Raftery, A. E. (1995). Bayesian model selection in social research. *Sociological Methodology*, *25*, 111–163. https://doi.org/10.2307/271063

Rickart, E. A. (2001). Elevational diversity gradients, biogeography and the structure of montane mammal communities in the intermountain region of North America. *Global Ecology and Biogeography*, *10*(1), 77–100. https://doi.org/10.1046/j.1466-822x.2001.00223.x

Rowe, R. J., Finarelli, J. A., & Rickart, E. A. (2010). Range dynamics of small mammals along an elevational gradient over an 80-year interval. *Global Change Biology*, *16*(11), 2930–2943. https://doi.org/10.1111/j.1365-2486.2009.02150.x

Sagarin, R. D., & Gaines, S. D. (2002a). The 'abundant centre' distribution: To what extent is it a biogeographical rule? *Ecology Letters*, *5*(1), 137–147. https://doi.org/10.1046/j.1461-0248.2002.00297.x

Sagarin, R. D., & Gaines, S. D. (2002b). Geographical abundance distributions of coastal invertebrates: Using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography*, *29*(8), 985–997. https://doi.org/10.1046/j.1365-2699.2002.00705.x

Sagarin, R. D., Gaines, S. D., & Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, *21*(9), 524–530. https://doi.org/10.1016/j.tree.2006.06.008

Sánchez-Cordero, V. (2001). Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. *Global Ecology and Biogeography*, *10*(1), 63–76. https://doi.org/10.1046/j.1466-822x.2001.00235.x

Santini, L., Pironon, S., Maiorano, L., & Thuiller, W. (2019). Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. *Ecography*, *42*(4), 696–705. https://doi.org/10.1111/ecog.04027

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, *185*(4145), 27–39.

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Siemers, B. M., & Schnitzler, H.-U. (2004). Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature*, *429*(6992), 657–661.

Tam, J. C., & Scrosati, R. A. (2011). Mussel and dogwhelk distribution along the north-west Atlantic coast: Testing predictions derived from the abundant-centre model. *Journal of Biogeography*, *38*(8), 1536–1545. https://doi.org/10.1111/j.1365-2699.2011.02498.x

Tang, Z.-Y., Wang, Z.-H., Zheng, C.-Y., & Fang, J.-Y. (2006). Biodiversity in China's mountains. *Frontiers in Ecology and the Environment*, *4*(7), 347–352. https://doi.org/10.1890/1540-9295(2006)004[0347:BICM]2.0.CO;2

Terborgh, J. (1971). Distribution on environmental gradients: Theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology*, *52*(1), 23–40. https://doi.org/10.2307/1934735

Terborgh, J., & Weske, J. S. (1975). The role of competition in the distribution of Andean birds. *Ecology*, *56*(3), 562–576. https://doi.org/10.2307/1935491

Virgós, E., Kowalczyk, R., Trua, A., de Marinis, A., Mangas, J. G., Barea-Azcón, J. M., & Geffen, E. (2011). Body size clines in the European badger and the abundant centre hypothesis. *Journal of Biogeography*, *38*(8), 1546–1556. https://doi.org/10.1111/j.1365-2699.2011.02512.x

Wang, Y.-Z., & Hu, J.-C. (1999). *The imitatively-colored pictorial handbook of the mammals of Sichuan*. China Forestry Publishing House. (In Chinese).

Wen, Z.-X., Cheng, J.-L., Ge, D.-Y., Xia, L., Lv, X., & Yang, Q.-S. (2018). Abundance-occupancy and abundance-body mass relationships of small mammals in a mountainous landscape. *Landscape Ecology*, *33*(10), 1711–1724. https://doi.org/10.1007/s10980-018-0695-z

Wen, Z.-X., Wu, Y.-J., Cheng, J.-L., Cai, T.-L., Du, Y.-B., Ge, D.-Y., Xia, L., & Yang, Q.-S. (2018). Abundance of small mammals correlates with their elevational range sizes and elevational distributions in the subtropics. *Ecography*, *41*(11), 1888–1898. https://doi.org/10.1111/ecog.03558

Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martinez, D., Agudo, R., & Monserrat, V. J. (2005). Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, *8*(12), 1138–1146. https://doi.org/10.1111/j.1461-0248.2005.00824.x

Yan, W.-B., Ji, S.-N., Shuai, L.-Y., Zhao, L.-G., Zhu, D.-P., & Zeng, Z.-G. (2019). Spatial distribution patterns of mammal diversity in Yangxian County of Shaanxi Province on the southern slope of the Qinling Mountains. *Biodiversity Science*, *27*(2), 177–185. (In Chinese).

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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