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Research

Abundance of small mammals correlates with their elevational range sizes and elevational distributions in the subtropics

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The idea that a positive abundance–range size relationship (ARR) is pervasive in nature has been challenged by recent studies focused on montane and island vertebrate assemblages. However, because some of these studies used species' local abundance and regional or global range size in examining the ARRs, the negative and neutral trends reported are questionable. Here, by relating species' mean abundance along elevational gradients to elevational range size, we examined the ARRs of non-flying small mammals on three subtropical mountains of southwest China. We also examined the relationship between mean abundance and elevational range centre (reflecting species' elevational distribution) on each mountain, and compared the elevational range centre and mean abundance between endemic and non-endemic species as they may have been subjected to different intensities of historical (e.g. geographical isolation and colonization) and ecological (e.g. ecological specialization) processes. The results show significantly positive relationship between mean abundance and elevational range size on each mountain. We also observed a consistent positive relationship between mean abundance and elevational range centre, probably due to the stronger local specialization of mid- and high-elevation species, lower species richness at higher elevations, and increasing extinction rate of small-ranged less abundant species towards higher elevations. A novel finding of our study is that endemic species show higher elevational range centres and higher mean abundance than non-endemic species on each mountain, which is most likely driven by the increasing geographical isolation with elevation and the higher degree of ecological specialization for endemic species. Measuring abundance and range size at the same spatial scale is a key prerequisite to evaluate the ARRs of montane small mammals.

Keywords: abundance–range size relationship, geographical isolation, elevation

Introduction

The phenomenon that more abundant species in a region tend to be more widely distributed than less abundant species is constant across groups of organisms, geographical regions and scales (Brown 1984, Blackburn et al. 1997, Gaston and Blackburn 2000, Faulks et al. 2015, Webb et al. 2017). This positive abundance–range size relationship (ARR) is regarded as one of the most ubiquitous pattern in macroecology, around which a series of important theories have been proposed (e.g. metapopulation theory, Hanski et al. 1993; unified theory, McGill and Collins 2003). Some commonly cited explanations for the positive ARR include sampling artifact (the range sizes of locally rare species are underestimated because they are more likely to be undetected during sampling; Gaston and Blackburn 2000), resource use and availability (species utilizing more abundant or a wider array of resources become more abundant and widespread; Brown 1984, Webb et al. 2017), vital rates (species with higher population growth rate can achieve higher abundance and occupy more sites; Holt et al. 1997) and dispersal (the positive relationship between abundance and occupancy is a result of dispersal between patches of suitable habitat; Hanski et al. 1993, Borregaard and Rahbek 2010).

However, recent studies have reported notable exceptions to this pattern, particularly those focused on vertebrate assemblages (mostly birds) in isolated natural systems such as mountain ranges and islands (Reif et al. 2006, Isaac et al. 2009, Ferenc et al. 2016, Reeve et al. 2016). The authors suggested that montane and island biotas are shaped by long-term geographical isolation and climatic stability (MacArthur and Wilson 1967, Fjeldså et al. 2012, Qu et al. 2014), leading to a high number of endemic (range-restricted) species with high local abundance. Nevertheless, because some of these studies were based on incompatible spatial scales, i.e. local abundances related to regional or global range sizes (Reif et al. 2006, Ferenc et al. 2016, Reeve et al. 2016), the non-positive (negative or no relationship) ARRs reported are questionable. Hypotheses aiming to explain the ARR are concerned with the correlation between abundance and range size measured at the same spatial scale (Gaston 1996), and most hypotheses (including sampling artefacts and neutral dynamics) would not predict any relationship between mean abundance measured locally in a small subset of the range and total (e.g. global and regional) range size. This is because the positive ARR is driven by highly right-skewed frequency distributions of both abundance and range size (Gaston and Blackburn 2000). One would therefore expect the overall relationship become especially noisy when there is a spatial mismatch between the two measurements. For example, the Indo-Pacific birds show completely opposite patterns of the ARR when their local abundances are related to range sizes measured at the global (negative, Reeve et al. 2016) and local (positive, Theuerkauf et al. 2017) scale. Likewise, in order to obtain a reliable ARR for montane vertebrate assemblages, species' local abundances (mean abundance along the gradient) need to be related with their local range sizes (elevational range size).

Although mountain shapes are diverse (Elsen and Tingley 2015, Körner et al. 2017), there is a generally positive trend of geographical isolation with increasing elevation (Steinbauer et al. 2016), affecting both species diversity patterns (Brown 2001, Wen et al. 2016a) and composition of montane assemblages. Steinbauer et al. (2016) recently discovered a global pattern of monotonic increase in the percentage of endemic plant species with increasing elevation, mainly explained by topography-drive isolation. Moreover, it has been shown for several taxa (Himalayan vascular plants, Vetaas and Grytnes 2002; frogs of the Hengduan Mountains, Fu et al. 2006) that the richness of endemic species peaks at much higher elevations than the richness of non-endemic species along the same elevational gradient. On tropical mountains, mammalogists have noticed that endemic non-flying small mammals are often confined to the middle and high elevations whereas widespread species occur primarily at the base (Sánchez-Cordero 2001, Rickart et al. 2011). Whether this pattern is shared by small mammals living in subtropical and temperate mountains or is peculiar to tropical areas is still an open question. Long-term adaptation to montane environmental conditions and relatively stable climate of mountain ranges might favor the high abundance of montane endemic species (Reif et al. 2006, Ferenc et al. 2016). Furthermore, non-endemic montane species normally have their range centres distant from mountain ranges, and most species become increasingly rare towards the edges of their geographical ranges (Borregaard and Rahbek 2010). If these two mechanisms play a role in the vertebrate community assembly, we would expect that endemic species being more abundant than non-endemic species on a mountain.

Compared to the well-explored ARR, studies about correlation between abundance and elevational distribution of species is very limited. Nevertheless, the only empirical evidence is from a montane bird assemblage study in west-central Africa. Ferenc et al. (2016) showed that the numbers of individuals per species at higher elevations are greater than those for species at lower elevations, and suggested that the stronger local specialization of mid- and high-elevation species, decreasing species richness with elevation, and the higher extinction rate of small-ranged less abundant species at higher elevations may explain this positive correlation between abundance and elevational distribution. In this study, we aim to expand our understanding of this potentially important biological relationship to subtropical montane small mammals.

Using an exhaustive dataset collected during the period of 2010–2014, we examined the ARRs of non-flying small mammals on three subtropical mountains of the Mountainous Region of southwest China. The goal of the study was to a) explore the relationship between species' mean abundance and elevational range size; b) test whether endemic species occupy higher elevation sites and are more abundant than

non-endemic species, and c) test whether species distributed at higher elevations are more abundant than species at lower elevations. In addition, to empirically assess the influence of different spatial scales on ARR, we relate species' mean abundance to both local (elevational) range size and national range size.

Material and methods

Study areas

The three mountains investigated in this study were the Gongga Mountain (Sichuan), Baima Snow Mountain (Yunnan) and Sejila Mountain (Tibet), which are all located within the Mountainous Region of southwest China (MRSC) (Fig. 1). They share similar geological histories, macroclimate condition (simultaneously influenced by the Asian monsoon climate and Qinghai-Tibetan Plateau climate) and mammalian fauna, but vary in altitude, local habitats and climate. As one of the world's 25 biodiversity hotspots, the MRSC harbors an enormous quantity of endemic mammalian species that occur in its different mountain ranges (Myers et al. 2000, Wen et al. 2016a, b) as well as widespread Asian species.

The Gongga Mountain is the second highest mountain in the MRSC with an extensive elevational range (1000 to 7556 m) where strikingly diverse climatic zones, vegetation communities and faunal assemblages are present (Zhang et al. 1997, Wu et al. 2013). Our 2010 survey of the Gongga Mountain

was conducted on its eastern slope (29°32′–29°36′N, 101°57′–102°10′E), primarily in the Hailuo Valley. The eight sampling sites were situated at elevations between 1200 and 4000 m and separated by a 400 m elevation interval, spanning all habitable vegetation belts of the gradient. The Baima Snow Mountain (main peak at 5429 m), as one of the southernmost permanently snow-capped mountains in China, supports a large number of endemic animal species that only occur on this mountain and adjacent areas (e.g. *Rhinopithecus bieti*, Zhu et al. 2016). Our 2012 study of the Baima Snow Mountain was performed on its eastern slope (27°37′–27°41′N, 99°22′–99°24′E) in the Samage Forest. In total, six elevation sites were surveyed at 300 m elevation intervals between elevations of 2500 to 3970 m (the interval between the two highest sites was 270 m due to the mountaintop). Detailed information on the climate and vegetation of the study areas on the Gongga and Baima Snow Mountains are given in Wu et al. (2013) and Wen et al. (2014). The Sejila Mountain (main peak at 5300 m) is on the southeastern border of the Qinghai-Tibetan Plateau, with the Yarlung Tsangpo Grand Canyon lying in its southeast (Luo 2008). Our 2014 investigation of the mountain was conducted on its eastern slope (29°37′–30°01′N, 94°39′–95°01′E), comprising nine sampling sites that covered an elevation range from 2000 to 4400 m and were separated from each other by a 300 m elevational distance. There are four main vegetation types along the elevational gradient: evergreen broad-leaf forest (< 2300 m); coniferous and broad-leaf mixed forest (2300–3100 m); dark coniferous forest (3100–4100 m);
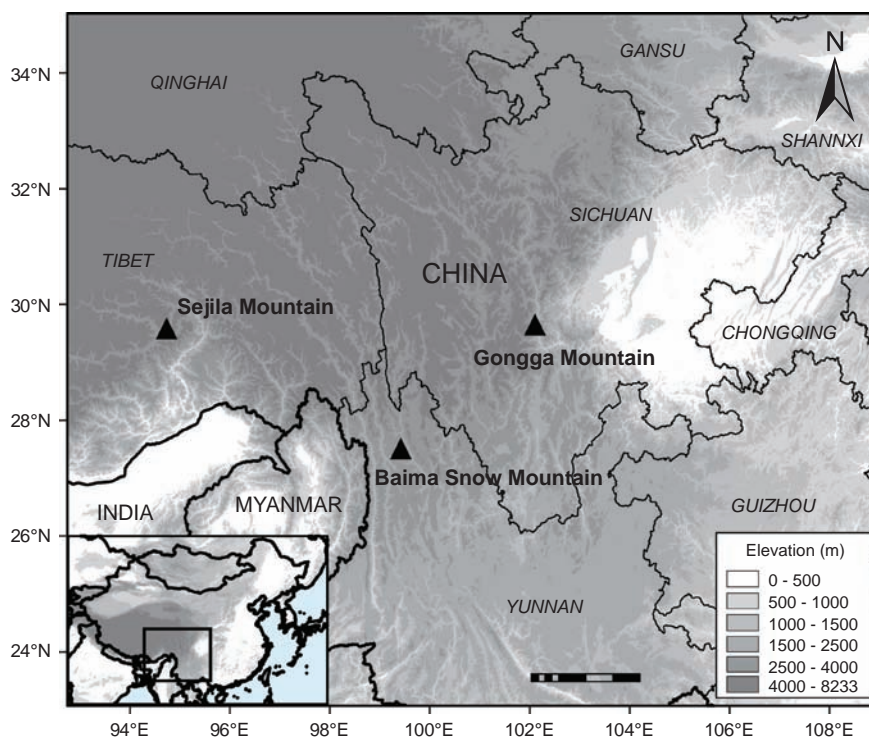

Figure 1. Locations of the three mountain ranges studied in the Mountainous Region of southwest China (MRSC).

alpine shrub and meadows (> 4100 m). Details of the sampling sites of each mountain are provided in Supplementary material Appendix 1 Table A1–A3.

Non-flying small mammal sampling

Non-flying small mammals on different mountains were surveyed using a standardized protocol. The focal orders were Erinaceomorpha, Soricomorpha, Rodentia and Lagomorpha. On each of the three mountains, we surveyed the sampling sites twice during the wet season (April to September), one in the early wet season (April to June) and the other in the late wet season (July to September), with the same sampling effort in each season.

At each elevation site on each mountain, we trapped across different microhabitats to maximize the number of non-flying small mammal species using iron snap traps (150 × 80 mm, Guixi Rattrap). Although the observed abundance of small mammals depends on the type of trap (Theuerkauf et al. 2011), the snap trap used in this study is efficient to sample virtually all small mammal species in the MRSC based on our long-term field experience (Wu et al. 2013, Wen et al. 2014). The traps were baited with fresh peanut and dried beancurd, and checked once a day in the early morning and re-baited if needed. We also set up the traps that sprung without capture (e.g. caused by rainfall) during the examination. The sprung traps might result in an underestimation of species' abundance, but the impact should be low due to the small number of sprung traps at each site. On the Baima Snow and Sejila Mountains, each elevation site consisted of six quadrats (the distances between quadrats were 25 to 35 m) surveyed for five consecutive nights in each sampling season, with each quadrat containing 50 traps arranged in a rectangular design (10 × 5 traps). The snap traps in the quadrat were placed 3–5 m apart. The survey on the Gongga Mountain was slightly different: each site had twelve quadrats, each containing 25 traps (5 × 5 traps) that were set up for six consecutive nights in each season (other sampling procudures follow as described previously). The trapping time was one night less on the Baima Snow and Sejila Mountains because the species accumulation curves plateaued within five nights. The different sampling method on the Gongga Mountain should not bias the observed pattern since the data from each mountain were analysed separately. In total, we conducted 28 800, 18 000 and 27 000 trap nights on the Gongga, Baima Snow and Sejila Mountains, respectively. Species' elevational range size and abundance were estimated based on a total of 2100 individuals of 38 non-flying small mammal species captured (Gongga, 676 individuals representing 23 species; Baima Snow, 720 individuals representing 23 species; Sejila, 704 individuals representing 17 species) along the elevational gradients on the three subtropical mountains (Supplementary material Appendix 1 Table A4–A6). Six species were shared among them, and the numbers of species unique to each mountain were six (Gongga), six (Baima Snow) and

seven (Sejila). Two arboreal species *Sciurotamias davidianus* and *Tamiops swinhoei* were not included in the following analyses because of the low efficiency of ground traps in capturing them.

Calculating abundance, elevational range size and elevational range centre

For each mountain, the abundance of each species at each elevation site was calculated by pooling the data of the early and late wet season, defined as the number of individuals per 100 trap nights (Heroldová et al. 2007). We used species' mean abundance to examine the ARR, which was calculated as the cumulative sum of abundances of each elevation site within the elevational range divided by the number of sites. The elevational range size of a species was defined as the range from the lowest to the highest site that a given species was captured. Although our study aimed to sample the small mammals at all the suitable elevations on each mountain, some species may potentially have a larger elevation range size than the sampled range because of the limitations in the sampling design (we only intensively sampled one slope of the mountain and the observed elevational range size is inevitably incomplete unless surveying the highest and lowest elevations of species, McCain 2009). Besides, on each mountain there were species sampled at a single elevation site so they had an observed elevational range size of zero, which was very likely smaller than the actual range. To address this potential pitfall, we added half of the maximum elevational distance between two adjacent sampling elevations (Gongga: 200 m; Baima Snow: 150 m; Sejila: 150 m) to each end of the recorded ranges of all species (Brehm et al. 2007, Wu et al. 2013). We calculated the elevational range centre of species using the equation

$$\Sigma_{i.n} E_i \times P_{Ai}$$

where $i.n$ are sites occupied by species A, E_i is the elevation (m) of site i, and P_{Ai} is the proportion of the individuals collected of species A at site i to the total number of individuals collected of species A along the entire elevational gradient (Menéndez et al. 2014). The elevational range centre has been weighted by species' elevational abundance (i.e. abundance at a given elevation) and thus more accurately reflects where most individuals of a species occur on a mountain.

Statistical analyses

Species' mean abundance values were log 10-transformed to meet the assumption of normality (the data are normally distributed according to Kolmogorov–Smirnov test, p > 0.05). For each mountain, we examined the relationship between mean abundance and elevational range size, and the relationship between mean abundance and elevational range centre using Pearson's correlations. In order to test whether

the inconsistency in the spatial scale of abundance and range size would affect the ARR pattern, we also related species' mean abundance to their national range sizes (i.e. the number of 1° × 1° grid cells occupied in China). We compared the mean abundance and elevational range centre between endemic and non-endemic species using independent-samples t-tests, defining endemic species as those distributed only in the MRSC and adjacent areas (Jiang et al. 2015). Pearson's correlations and independent-samples t-tests were performed in the R environment (ver. 3.2.2, R Development Core Team). We examined the elevational pattern of species richness on each mountain, and species were assumed to occur at any elevations between their observed upper and lower range limits (Wen et al. 2014).

As conventionally done in previous studies (Komonen et al. 2013, Reeve et al. 2016), we related species' elevational range sizes, elevational range centres and endemicity (endemic or non-endemic) to mean abundance using linear models (there was no collinearity among factors) for each mountain. For the response variable mean abundance, seven candidate models containing all possible combinations of the three explanatory variables were fitted. The performance of the models were evaluated using the Akaike's information criterion (AIC_C) (Burnham and Anderson 2002). Model selection was performed using the R package 'MuMln' (Bartoń 2015).

Although we have added a buffer to the observed elevational range size of each species, the elevational range sizes of some species might still be underestimated if they greatly exceeded the range of the sampled elevational gradient. An effective solution to this problem is to focus only on species that are entirely distributed within our sampling sites. Therefore, we performed additional analyses using only species that were captured between the second highest and the second lowest sampling sites to examine the relationships between mean abundance and elevational range size, elevational range centre and national range size, and to determine if endemic and non-endemic species differed in mean abundance and elevational range centre. The numbers of qualified species were 12 on the Gongga Mountain, four on the Baima Snow Mountain and 10 on the Sejila Mountain.

Data deposition

Data available from the Dryad Digital Repository: < http:// dx.doi.org/10.5061/dryad.26s8n73 > (Wen et al. 2018).

Results

Species' mean abundance was positively associated with elevational range size on each mountain, and all of the relationships were statistically significant (Fig. 2a, b, c). Similarly, there was a consistent positive correlation between mean abundance and elevational range centre. The relationship was significant on the Baima Snow Mountain (Fig. 2d, e, f). However, a weak negative relationship was found between species' mean abundance and national range size on each of the

three mountains (Fig. 2g, h, i). On all mountains, the mean abundance of endemic non-flying small mammals (mean ± SE, Gongga: 0.14 ± 0.07; Baima Snow: 0.28 ± 0.15; Sejila: 0.22 ± 0.07) was higher (Gongga: p=0.263; Baima Snow: p=0.022; Sejila: p=0.001) than that of non-endemic small mammals (Gongga: 0.08 ± 0.03; Baima Snow: 0.08 ± 0.02; Sejila: 0.05 ± 0.02) (Fig. 3a), and the elevational range centre of endemic species (Gongga: 2436 ± 172 m; Baima Snow: 3109 ± 80 m; Sejila: 3048 ± 175 m) was higher (Gongga: p=0.234; Baima Snow: p=0.285; Sejila: p=0.746) than that of non-endemic species (Gongga: 2392 ± 217 m; Baima Snow: 2998 ± 124 m; Sejila: 2729 ± 264 m) as well (Fig. 3c). Small mammals showed a hump-shaped elevational richness pattern on the Gongga Mountain, whereas a low plateau richness pattern was observed on both the Baima Snow and Sejila mountains (Fig. 4).

The best models (delta AIC_C < 2) to explain species' mean abundance in each mountain include elevational range size. Yet, the results of AIC_C weight suggested that elevational range centre and endemicity also affected mean abundance (Table 1).

The exclusion of the species found on the extremes of the elevational gradients had little influence on the results. We found a consistent (significant on the Gongga Mountain) positive relationship between mean abundance and elevational range size on each mountain. Mean abundance was positively correlated with elevational range centre on the Gongga and Baima Snow Mountains, while the relationship was neutral on the Sejila Mountain. There was no evident relationship between mean abundance and national range size across mountains. On each mountain, endemic species exhibit higher elevational range centres and higher mean abundance than non-endemic species (Supplementary material Appendix 2 Fig. A1–A2).

Discussion

Positive ARR

With evidence from three subtropical mountains in the MRSC, we have shown a significantly positive ARR for the non-flying small mammal assemblages along elevational gradients. Our finding is consistent with most of the previous continental studies concerning the ARR in mammals, including Australian marsupials (Johnson 1998), British mammals (Blackburn et al. 1997, Holt and Gaston 2003), Madagascan and African primates (Harcourt et al. 2005) and Finnish small mammals (Komonen et al. 2013).

Conversely, it has been indicated that tropical montane (Reif et al. 2006, Ferenc et al. 2016) and island (Reeve et al. 2016) birds tend to exhibit a negative or neutral ARR. The authors suggest that the predominance of endemic, small-ranged species in these regions caused by geographical isolation and climatic stability might explain to the non-positive ARRs. However, a mismatch between the spatial scales of range size (local) and of the mean abundance (regional or
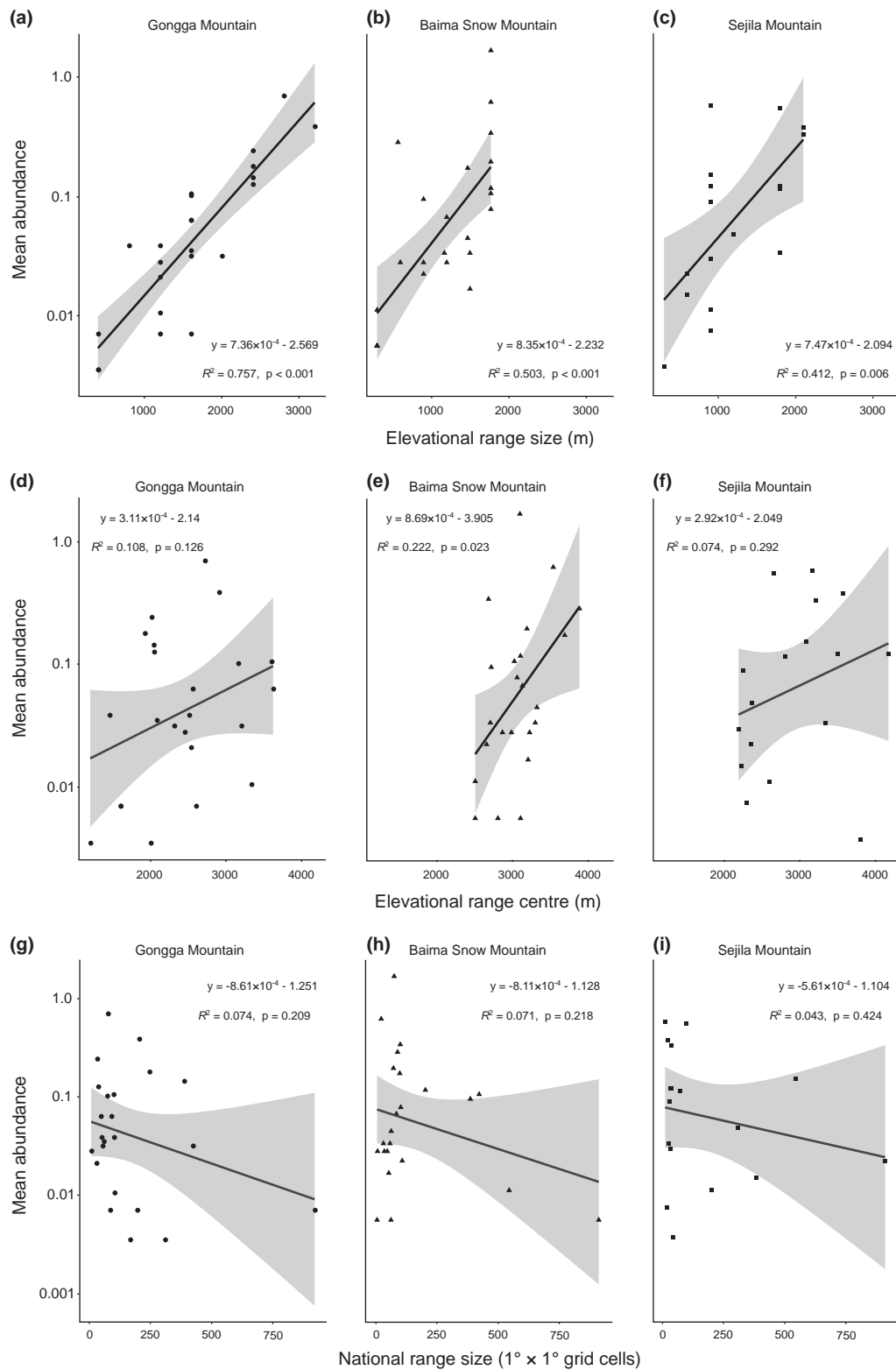
Figure 2. The relationships between mean abundance (the number of individuals per 100 trap nights) and elevational range sizes (m) (a, b, c), elevational range centres (m) (d, e, f), national range sizes (the number of $1° \times 1°$ grid cells occupied in China) (g, h, i) of non-flying small mammals on the Gongga, Baima Snow and Sejila Mountains. The data points represent individual species (Gongga: 23, Baima Snow: 23, Sejila: 17). The significant relationships (p < 0.05) are shown by black lines and non-significant relationships are shown by dark grey lines. The linear regression equation, R^2 and p value of each relationship are shown. The grey zones are 95% confidence intervals. Note log scale is used on the y axis.
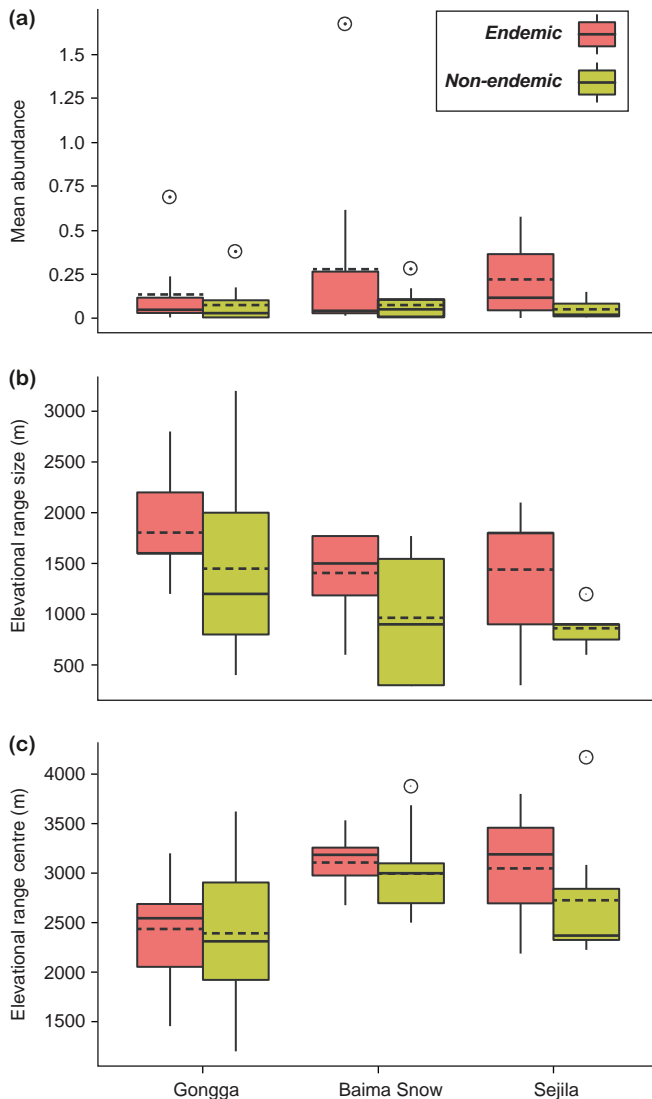
Figure 3. Mean abundance (the number of individuals per 100 trap nights) (a), elevational range sizes (m) (b), and elevational range centres (m) (c) of endemic (Gongga: 10, Baima Snow: 11, Sejila: 10) and non-endemic (Gongga: 13, Baima Snow, 12; Sejila: 7) non-flying small mammals on the Gongga, Baima Snow and Sejila Mountains. The box-and-whisker plots illustrate the median (solid line inside the box), mean (dashed line), 25th and 75th quartiles (lower and upper boundaries of the box) and 10th and 90th quartiles (whiskers). The outliers are shown as filled circles.

global) used in these studies hampers reliable inferences. Recently, Theuerkauf et al. (2017) argued that the negative ARRs in Indo-Pacific bird communities reported by Reeve et al. (2016) were incorrect because local abundances were related to global distributions. When using species' local ranges, the bird communities instead showed a remarkably positive ARR (Theuerkauf et al. 2017). In our case, the positive ARR was derived from relating species' abundance (mean abundance along the elevational gradient) with range sizes (elevational range size) at the same scale. Likewise, when we used the national species range sizes to fit the ARR, the

significantly positive trends disappeared and were replaced by weak negative relationships.

Endemic vs non-endemic

An intriguing finding of our study is that endemic non-flying small mammals occupy higher elevation sites and are more abundant than non-endemic ones. For montane small mammals, Brown (2001) hypothesized that the increasing geographical isolation with elevation should lead to a higher level of endemism towards higher elevations due to reduced dispersal and lower rate of colonization, which accords with our data. The similarity across the Gongga, Baima Snow and Sejila mountains is notable given the shared geological and mammalian faunal histories. Among the many geological processes that shaped the modern biodiversity patterns of east Asia, the dramatic tectonic uplift of the MRSC in the late Miocene and Pliocene was a fundamental event (Fjeldså et al. 2012, Favre et al. 2015). It gave rise to numerous high, island-like mountains (most > 3000 m, including our study areas) spatially isolated from one another by deep valleys, among which diversification and speciation occurred (He and Jiang 2014). The isolation was particularly strong at the high and middle elevations, facilitating the emergence of endemic non-flying small mammals (Wen et al. 2016a).

Several factors may explain the higher abundance of endemic species than non-endemic species. First, endemic and non-endemic species have different degrees of ecological specialization to local environments. The mountains of the MRSC harbored abundant climatically stable habitats during Pleistocene climatic oscillations (glacial-interglacial variations) (Qu et al. 2014, Wen et al. 2016b, Wu et al. 2017). Specialization under long-lasting favorable climates allows endemic montane species to maintain a stable population. By comparison, although non-endemic species usually show wider distribution and occur in diverse habitats in subtropical regions (Walter 1971), they may not be able to establish a large-sized population in a mountainous region with unique high topographical complexity and ecological heterogeneity. Reif et al. (2006) showed that non-endemic birds have narrower local niches than endemic and non-endemic montane birds on Bamenda Highland of Cameroon, while the situation was reversed at the regional scale. We noticed that on each of our studied mountains, the individuals of the *Rattus* species (*Rattus norvegicus*, *Rattus nitidus*, *Rattus losea* and *Rattus tanezumi*) were relatively scarce (Supplementary material Appendix 1 Table A4–A6) despite their prevalence in south China. This result suggests that non-endemic species are less adapted to local subtropical montane habitats, despite that most *Rattus* species are commensal animals favoured by human-modified habitats. Second, if the MRSC is located at the range edges of many non-endemic species, it is expected that they have lower abundance as it generally decreases from the center towards the edge of species range (Brown 1984, Samis and Eckert 2007, Ren et al. 2013). Third, because the priority effect
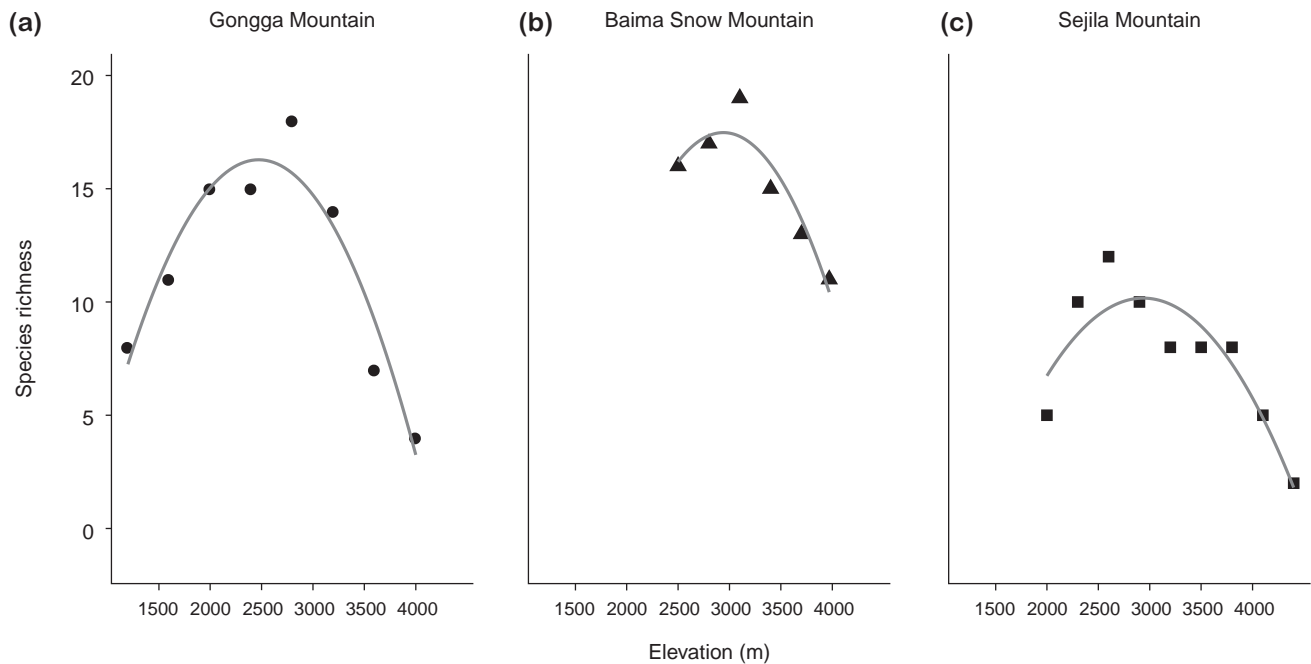
Figure 4. Elevational patterns of species richness of non-flying small mammals on the Gongga (a), Baima Snow (b) and Sejila (c) mountains.

(i.e. endemic or early colonizing species negatively impacts the subsequently colonizing species by reducing the availability of space and recourses, Chase 2003) plays a role in the assembly of montane small mammal communities (Wen et al. 2016a), endemic species may gain a competitive advantage over non-endemic counterparts and therefore become more abundant. Last, given that species richness is generally lower at higher elevations, there are more resources available for individual high-elevation species due to reduced interspecific competition (density compensation

Table 1. The possible models relating species' mean abundance (the number of individuals per 100 trap nights, log 10-transformed) to elevational range size (m), elevational range centre (m) and endemicity (endemic/non-endemic) of the non-flying small mammals on the Gongga (n=23), Baima Snow (n=23) and Sejila (n=17) Mountains in the MRSC. Model's performances were evaluated using the Akaike's information criterion (AIC_C), with a lower value indicating a better fit.

Variables included in the model	AIC_C	delta AIC_C	AIC_C weight
Gongga Mountain			
Elevational range size	−31.3	0	0.663
Elevational range size + elevational range centre	−28.39	2.91	0.155
Elevational range size + endemicity	−28.35	2.95	0.152
Elevational range size + elevational range centre + endemicity	−25.09	6.21	0.03
Endemicity	−14.41	16.89	0.002
Elevational range centre	−14.19	17.11	0.001
Elevational range centre + endemicity	−12.04	19.26	0.001
Baima Snow Mountain			
Elevational range size	20.3	0	0.332
Endemicity	22.04	1.74	0.139
Elevational range size + endemicity	22.68	2.38	0.101
Elevational range size + elevational range centre	22.96	2.66	0.088
Elevational range centre	23.07	2.77	0.083
Elevational range centre + endemicity	24.34	4.04	0.044
Elevational range size + elevational range centre + endemicity	25.73	5.43	0.022
Sejila Mountain			
Elevational range size	−5.9	0	0.292
Endemicity	−5.62	0.28	0.254
Elevational range size + endemicity	−3.81	2.09	0.103
Elevational range size + elevational range centre	−2.83	3.07	0.063
Elevational range centre	−2.76	3.14	0.061
Elevational range centre + endemicity	−2.52	3.38	0.054
Elevational range size + elevational range centre + endemicity	0.09	5.99	0.015

theory, MacArthur et al. 1972). Thus, the higher elevational distribution of endemic species may enable them to utilize more resources and expand their populations.

Positive relationship between mean abundance and elevational range centre

Our study shows that species' mean abundance is positively related to elevational range centre. Similar positive trends in all sampled mountains reported here suggest a general ecological pattern for montane mammals. Likewise, Ferenc et al. (2016) reported a strong positive correlation between the mean abundance and elevational midpoint of passerine birds on Mt Cameroon. They ascribed the positive correlation to three main reasons: higher degree of ecological specialization of high-elevation species; decreasing species richness with elevation that leads to less interspecific competition for resources and thus higher abundance per species at higher elevations; and stronger extinction filters at higher elevations tend to eliminate species with both small ranges and small populations, leaving common small-ranged and large-ranged species and rare large-ranged species in the community (Johnson 1998). These factors may also contribute to the patterns found in our study, particularly the first one because endemic species occupy higher elevation sites on each mountain. Further, the low plateau elevational richness pattern found on the Baima Snow and Sejila mountains indicates the higher abundance at higher elevations could be resulted from the lower number of species. In addition, the decreasing diversity and abundance of predators (e.g. raptors and snakes) with elevation (Kumar et al. 2009) is another explanation for the higher abundance of high-elevation species. For example, Fu et al. (2007) found that snake species richness in the Hengduan Mountains (which constitutes the main part of the MRSC) shows a monotonically decreasing trend from 1500 to 4400 m.

Conclusion

The pattern and driving force behind the ARR on subtropical mountains deserve particular attention because of the extremely high levels of species diversity and endemism. Our study reveals a significantly positive relationship between the mean abundance and elevational range size of non-flying small mammals on three subtropical mountains of the MRSC, and a consistent positive relationship between mean abundance and elevational range centre. We empirically show that using inconsistent spatial scales of species mean abundance and range size to assess ARR lead to an inaccurate pattern. Noteworthy, endemic species occupy higher elevation sites and are more abundant than non-endemic species, which is most likely driven by the increasing geographical isolation with elevation and the higher degree of ecological specialization of endemic species. Future studies addressing the ARRs of mammals on tropical and temperate mountains, and the ARRs of other vertebrates (e.g. amphibians and birds) on subtropical mountains will enable us to better appreciate this well-known but little understood macroecological relationship.

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Supplementary material (Appendix ECOG-03558 at < www.ecography.org/appendix/ecog-03558 >). Appendix 1–2.