

The relationship between species elevational range size of breeding birds, temperature range, primary productivity, habitat heterogeneity, and species richness: an empirical test of related environmental hypotheses and rescue effect in the Eastern Himalayas

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Abstract

Describing the pattern and variations in spatial pattern of biodiversity and revealing its underlying mechanisms remain a central focus in ecology. However, less attention was paid to the species range size, and few studies have explored the drivers of species range size and the relationship between species range size and species richness (rescue effect). Here, we use a comprehensive dataset of breeding birds collected from 2018 to 2019 along the elevational gradient in Lebu Valley, Eastern Himalayas of China to explore the a) species mean elevational range size pattern, b) drivers influencing species mean elevational range size, and c) rescue effect. We found that species mean elevational range size of birds in Lebu Valley was a hump-shaped pattern (species mean elevational range size was largest at middle elevations), and the annual temperature range and normalized vegetation index were the most important explanatory variables for the species mean elevational range size pattern. However, species mean elevational range size was negatively correlated with the annual temperature range and positively correlated with the normalized vegetation index, respectively. These results were contrary to the predictions of the climate variability hypothesis and the ambient energy hypothesis. In addition, the correlation between species mean elevational range size and habitat heterogeneity was weak, which indicated that the habitat heterogeneity hypothesis also failed to predict the breeding bird mean elevational range size pattern in Lebu Valley. Moreover, we found the hump-shaped species richness pattern, which could also be resulted from non-directional rescue effect. Given the uncertainty in mean elevational range size pattern and the fact that much of the previous research has rarely tested the relationship between species range size and richness patterns, hypotheses explaining the elevational range size and the underlying mechanisms should be tested in more studies of different taxa and regions.

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ABSTRACT

Describing the pattern and variations in spatial pattern of biodiversity and revealing its underlying mechanisms remain a central focus in ecology. However, less attention was paid to the species range size, and few studies have explored the drivers of species range size and the relationship between species range size and species richness (rescue effect). Here, we use a comprehensive dataset of breeding birds collected from 2018 to 2019 along the elevational gradient in Lebu Valley, Eastern Himalayas of China to explore the a) species mean elevational range size pattern, b) drivers influencing species mean elevational range size, and c) rescue effect. We found that species mean elevational range size of birds in Lebu Valley was a hump-shaped pattern (species mean elevational range size was largest at middle elevations), and the annual temperature range and normalized vegetation index were the most important explanatory variables for the species mean elevational range size pattern. However, species mean elevational range size was negatively correlated with the annual temperature range and positively correlated with the normalized vegetation index, respectively. These results were contrary to the predictions of the climate variability hypothesis and the ambient energy hypothesis. In addition, the correlation between species mean elevational range size and habitat heterogeneity was weak, which indicated that the habitat heterogeneity hypothesis also failed to predict the breeding bird mean elevational range size pattern in Lebu Valley. Moreover, we found the hump-shaped species richness pattern, which could also be resulted from non-directional rescue effect. Given the uncertainty in mean elevational range size pattern and the fact that much of the previous research has rarely tested the relationship between species range size and richness patterns, hypotheses explaining the elevational range size and the underlying mechanisms should be tested in more studies of different taxa and regions.

KEYWORDS

breeding birds, elevational range size, Himalayas, rescue effect, species richness

INTRODUCTION

Describing the pattern and variations in spatial pattern of biodiversity and revealing its underlying mechanisms remain a central focus in ecology. With the popularization of the concept of biodiversity (e.g., species richness), related research is developing rapidly (Wilson & Ehrlich, 1991). But less attention has been paid to the ultimate cause of species richness: species range size (e.g., geographic distribution, latitudinal range, elevational range). The degree of overlap of the range size forms the species richness pattern we have observed, and the higher the degree of overlap of species range in a certain area, the higher the species richness. Moreover, species range size can reflect the niche of species (Pfenninger, Nowak, & Magnin, 2007). It is also correlated with the formulation in species protection strategies (Herzog, Oswaldo, Embert, Caballero, & Quiroga, 2012), especially the conservation of faunas (Kevin J Gaston, 1996) and the assessment of the probability of extinction (Price, Helbig, & Richman, 1997). However, the underlying mechanism shaping species range size is unclear (Kevin J Gaston, 1998; Webb & Gaston, 2003).

Most studies on species range size focused on examining the positive relationship between communities range size (species mean range size) and elevation (or latitude), which is called Rapoport's rule (Rapoport, 1975, 1982; Stevens, 1989, 1992; Böhm et al., 2017; Colwell & Hurltt, 1994; Kevin J Gaston, 1999; K J Gaston, Blackburn, & Spicer, 1998; Hausdorf, 2006; McCain & Knight, 2013; Rohde, Heap, & Heap, 1993; Zhou et al., 2019). However, few studies have explored the drivers of species range size (but see J.-Y. Kim et al., 2019; Letcher & Harvey, 1994; Luo et al., 2011; Stevens, 1989, 1992). Species range size could be related to different factors such as climate, ambient energy, and habitat heterogeneity which referred to the climate variability hypothesis, the ambient energy hypothesis, and the habitat heterogeneity hypothesis. The climate variability hypothesis states that species living in areas with larger variations in climatic conditions (e.g., temperature) tend to have wider tolerances; that is, climate stability is negatively correlated with species range size (Stevens, 1989, 1992). The ambient energy hypothesis predicts that environmental energy (e.g., productivity) determines the degree of overlap of species range size (Kerr & Packer, 1997). For example, species' interaction is more frequent in the tropical regions, as the tropical regions receive more environmental energy than the temperate regions (environmental energy is negatively related to latitude), which can support finer niche separation and the coexist of more species, leading to smaller species range size (Brown, 1981). The habitat heterogeneity hypothesis, which is an extension or supplement of the ambient energy hypothesis, states that the greater heterogeneity of the spatial and topographical habitat structure allows for finer subdivision of restricted energy, suggesting that the higher the habitat heterogeneity, the smaller the species range size could be (species range size, to some extent, is a surrogate of species niche) (J.-Y. Kim et al., 2019). However, the influence of habitat heterogeneity on the species range size may be closely related to the combination of habitat types (Hu et al., 2017). The fit of these hypotheses above to different taxonomic groups and gradients is still uncertain and needs to be further tested in more biogeographical regions.

Local species richness can be strongly impacted by the proximity of the species' range margins of potentially interacting species. The higher the degree of the proximity of the species' range margins of potentially interacting species (which can be defined as inflow intensity, J.-Y. Kim et al., 2019) can increase the species richness. This phenomenon was called rescue effect (Stevens, 1992). Moreover, different shapes of richness patterns (e.g., monotone decreasing and unimodal pattern) may be influenced by kinds of rescue effects (i.e., Steven's rescue effect, alternative rescue effect, and non-directional rescue effect). The premise of Steven's rescue effect (or Rapoport's rescue effect) is that if species in high elevation (or latitude) region have a larger range size (the distribution of species range size follows the Rapoport's rule), species overlap in low elevation (or latitude) region will increase (species from higher elevation or latitude tend to inflow to low elevation or latitude) (Stevens, 1992). While alternative rescue effect proposes that decreasing species richness along elevation or latitude could result from differential upper limits of species with source populations below mid-point of the gradient even if the species have a larger range size in the low elevation or latitude (Almeida-Neto, Machado, Pinto-da-Rocha, & Giaretta, 2006). Besides, non-directional rescue effect (Almeida-Neto et al., 2006) argued that species from both ends of a gradient (if species from both high and low elevation have larger range sizes) would lead to an increase of species richness in the middle elevation and resulting in a unimodal species richness pattern.

Mountain ecosystems are hot spots in biological diversity (Lomolino, 2001). The environmental conditions (e.g., climate, habitat, and productivity) vary remarkably along elevations over small spatial extents, making elevational gradient an outstanding natural laboratory for studies in ecology and biogeography. Here, we used a comprehensive dataset of breeding birds collected from 2018 to 2019 along an elevational gradient in the Eastern Himalayas of China. Our objectives were to a) assess how species mean elevational range size changes along elevation; b) explore the drivers influencing species mean elevational range size; c) explain the relationship between species range size and species richness (rescue effect) to expand our understanding of underlying mechanisms of community structure and species richness pattern.

MATERIALS AND METHODS

Study areas

Lebu Valley (27°49'-28deg00'N, 91deg41'-91deg52'E; Figure 1) is located in the Eastern Himalayas (one of

the 34 biodiversity hotspots all over the world. Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011), China. ranging from 2,300 m above sea level (a.s.l.) to 5,000 m a.s.l. The planimetric distance from the bottom of the valley to the summit of Mt. Xiala is about 46 km. There are five vegetation types along the elevational gradient in Lebu: broadleaved deciduous forest (2,300-2,900 m a.s.l.), coniferous and broad-leaf mixed forest (2,900-3,400 m a.s.l.), dark coniferous forest (3,400-3,800 m a.s.l.), alpine shrub and meadows (3,800-4,400 m a.s.l.), and alpine meadow (4,400-5,000 m a.s.l.) (Wang et al., 2020).

Bird sampling

Bird species were sampled along the elevational gradient from 2,350 m and 4,950 m a.s.l. using the line transect method. Field sampling could not be done lower or higher because of the inaccessible topographies such as cliffs and glaciers. The entire 2,600 m elevational gradient was divided into 26 consecutive 100-m elevational bands. One transect (the length of each transect was 2.5 km) was placed in each elevational band (for a total of 26 transects, Figure 1). Bird censuses were carried out between 20 min after dawn and 10:00 hours and between 16:00 hours and 20 min before sunset (local time) by the same proficient observers. Birds within 50-m of the observers were recorded. The transects were sampled in a random order to reduce the temporal autocorrelation. Replicated bird censuses were made four times during the breeding season, from June to August 2018 and June to July 2019. For each transect, we made two replicated surveys in the morning and two at dusk, respectively. The taxonomic system of birds was followed Zheng (2011) (Zheng, 2011). We used breeding birds (including residents and summer migrants) for statistical analyses because seasonal and long-distance migratory birds could cause potential bias.

We interpolated the presence of species to 26 elevational bands according to their lowest and highest observed presences as the relatively small study area and strong movement ability of birds. This interpolation method is often used in elevational studies, and it can reduce the bias of underestimation of species richness due to insufficient sampling. We used species accumulation curves to evaluate whether species diversity was sampled sufficiently. If the species accumulation curve becomes an asymptote after a sharp rise and the rise is slow, the sampling is sufficient (Ugland, Gray, & Ellingsen, 2003). Estimator (Chao2) was used to compute estimated species richness. The Chao2 statistics of each 100-m elevational band were calculated in EstimateS 9.10 (<http://purl.oclc.org/estimates>) (R K Colwell, 2013). Pearson correlation analysis was used to assess the relationship between observed species richness and Chao2 to assess how well the species richness was sampled within each 100-m elevational band.

Species mean elevational range size pattern

Species elevational range size is defined as the range from the lowest to highest elevation of a given species. Species only recorded in one site (elevational range size is zero) were considered to occur in the entire 100-m elevational band (Stevens, 1992); elevational range sizes less than 100 m were also adjusted to 100 m considering the mobility of bird species. Three different methods were used to calculate the mean elevational range size of species in each 100-m elevational bands respectively: (1) the average range size of all species within each elevational band (the Steven’s method, Stevens, 1992); (2) the average range size of species whose midpoints occur in each elevational band (the midpoint method, Rohde et al., 1993); (3) the average range size of species whose abundance center (Equation 1) occur in each elevational band (the specimen method, Almeida-Neto et al., 2006); abundance center is calculated as the weighted average midpoint of each species, as follows:

$$WA_i = \frac{\sum_{i=1}^n E_i N_i}{\sum_{i=1}^n N_i} \text{ (Equation 1)}$$

where WA_i is the weighted average midpoint of species i ; E_i is the elevation of each band where species i is present; and N_i is the number of individuals of species i at each elevational band (Almeida-Neto et al., 2006).

Drivers of species mean elevational range size

Three environmental factors (annual temperature range, normalized difference vegetation index, and habitat heterogeneity) related to the climate variability hypothesis, the ambient energy hypothesis, and the habitat heterogeneity hypothesis, were obtained for each 100-m elevational band.

Annual temperature range

We use the annual temperature range (ATR) as the independent variable for the climate variability hypothesis. To catch the precise characteristics of climate, we set seven mini weather stations in Lebu Valley (2,440, 2,822, 2,914, 3,311, 3,499, 4,219, 4,504 m a.s.l.). Each mini weather station concluded two data loggers (HoBo Pro- RH/Temp and HoBo Pro-Precipitation/Temp) (Half a meter above the ground) and was surrounded by fences to keep interference from wild animals. Annual temperature maximum and annual temperature minimum were recorded from 2018 to August 2019. ATR was calculated as the annual temperature maximum minus annual temperature minimum and then extrapolated to 26 elevational bands using the simple ordinary least square (OLS) regression.

Normalized difference vegetation index

Normalized difference vegetation index (NDVI) was used as a proxy for net primary productivity in this study. We extracted NDVI data (1-km² resolution) of January, April, July, and October for 4 consecutive years (2009-2012) in the Lebu Valley from the Computer Network Information Center, Chinese Academy of Sciences (CNIC, CAS) (<http://www.gscloud.cn>; date of the download: 2016/6/17).

Habitat heterogeneity

We extracted the land-cover type from the GlobeLand30 (<http://www.globallandcover.com>; date of the download: 2019/3/25). We calculated

the number of land-cover types in each 1-km² grid cell. Ten land-cover types were classified by GlobeLand30. We combined a 30-m DEM and the 30-m landcover data of the study area to obtain the landcover type in each 100-m elevational band. We extracted the cells of the landcover raster data that correspond to the areas defined by the 30-m DEM for each 100-m elevational band using the extract by mask tool in ArcGIS 10.4. We set the cell size of the result as the input DEM data. In Lebu Valley, five landcover types (Cropland, Forest, Grass, Water, and Ice) were defined. We calculated the habitat heterogeneity (HH) using the Shannon diversity index. We also tested the relationship between HH and the area percentage of suitable habitat types (forest and grass). We compared the elevational pattern of the area percentage of suitable habitat types and HH to test whether the area percentage of suitable habitat types is large when the value of HH is high.

Inflow intensity

We classified species into two groups: low abundance center group and high abundance center group based on the location of their abundance center (Equation 1). Species with abundance center below the midpoint of the elevational gradient of Lebu Valley (3,650 m a.s.l.) are defined as the low abundance center group. Species with abundance center above the midpoint of the elevational gradient are defined as the high abundance center group. Inflow intensity is defined as the difference between the mean abundance center (m) of the low abundance center group and the high abundance center group in each 100-m elevational band ($\text{mean abundance center}_{\text{high group}} - \text{mean abundance center}_{\text{low group}}$) (J.-Y. Kim et al., 2019). In elevational bands where only species of one group (high or low abundance center group) were found, the value of the inflow intensity was zero. If the inflow intensity is positively correlated with species richness, the proximity of the range margins of potentially interacting species was considered to contribute to the richness pattern, which indicates that the rescue effect was supported (J.-Y. Kim et al., 2019).

Statistical analyses

We performed polynomial regression analyses to assess the form of the patterns of species mean range size as a function of elevation along the gradient. Best-fit models were selected based on the corrected Akaike's information criterion (AICc). To choose the most appropriate method (the Steven's method, the midpoint

method, and the specimen method) to describe the mean elevational range size pattern, we compared the Goodness of Fit (R^2) between the best models. Then we chose the model with the highest R^2 and used this method to calculate the species mean elevational range size for subsequent analyses.

Multiple regression analyses were conducted to explain species mean elevational range size. The dependent variable was species mean elevational range size of each 100-m elevational band (according to the Steven's method). ATR, NDVI, and HH were used as independent variables. Based on the lowest AICc value, the best models ($\Delta AICc < 2$) were selected from the 7 models representing all possible combinations of the 3 independent variables. OLS linear regression model was also fitted to test the relationship between the area percentage of suitable habitat types and HH and the relationship between inflow intensity and species richness.

The polynomial regression analyses were performed in the PAST 3.0 (<http://folk.uio.no/ohammer/past/>) (Hammer, Harper, & Ryan, 2001). Correlation analysis, OLS regression models, multiple regression analyses, and model selection were performed in the SAM 4.0 (<http://www.ecoevol.ufg.br/sam/>) (Rangel, Dinizfilho, & Bini, 2010).

RESULTS

Sampling effort

A total of 123 breeding birds were recorded in our field surveys (Figure 2). All accumulation curves for each 100-m elevational band reached a plateau or an asymptote (Figure S1 in Appendix 2). Moreover, the observed species richness was highly correlated with Chao2 value ($R = 0.82$). Both accumulation curves and correlation analysis indicated that the sampling effort within 26 elevational bands was adequate.

Species mean elevational range size pattern

Consistent elevational hump-shaped patterns of species mean range size were found across different measurements (guided by the lowest AICc value, elevational range size pattern better fitted by a cubic equation than a linear or quadratic equation) (Table 1). Species mean range size increased with elevation, reached a peak at mid-elevation, and then decreased (Figure 3). The Steven's method was the best-fitted method with the largest R^2 ($R^2 = 0.80$, $P < 0.01$ Figure 3a) value compared to the midpoint method ($R^2 = 0.78$, $P < 0.01$ Figure 3b) and the specimen method ($R^2 = 0.45$, $P < 0.01$ Figure 3c). The species mean elevational range size calculated by the Steven's method was used in the multiple linear regression models explaining species mean elevational range size.

Drivers of species mean elevational range size

The elevational pattern of ATR increased monotonically; NDVI increased rapidly at low elevation, with a stable plateau at middle elevation, then decreased slowly with the increasing elevation; HH increased with fluctuations and peaked at middle elevation (Figure S2 in Appendix 2).

The best models ($\Delta AICc < 2$) showed that ATR and NDVI were the most significant explanatory variable. ATR was negatively correlated with species mean elevational range size, and NDVI was positively correlated with species mean elevational range size (Table 2).

HH was a relatively weak explanatory variable of species mean elevational range size, and the area percentage of suitable habitat types was irrelevant with HH along elevation ($R^2 = 0.17$, $P = 0.04$; Figure S3a in Appendix 2). The area percentage of suitable habitat types peaked at 2,350 m to 2,950 m a.s.l. and 3,650 m to 4,050 m a.s.l. (Figure S3b in Appendix 2), where the values of HH were the lowest.

Relationship between inflow intensity and species richness

The species richness was positively correlated with inflow intensity along elevation in Lebu Valley ($R^2 = 0.31$, $P < 0.01$; Figure 4a). Species richness along elevation in Lebu Valley showed a hump-shaped pattern (Figure 4b)—better fitted by a cubic equation of elevation than a linear equation and quadratic equation (the AICc value was 197.55 for the linear equation, 157.44 for the quadratic equation, and 139.93 for the cubic equation).

The species richness “hump” occurred from 2,750 to 3,650 m a.s.l. Species from both ends of the elevational gradient in Lebu Valley would contribute to the observed hump-shaped species richness pattern.

To test whether the proximity of the range margins of potentially interacting species from both sides of the “hump” of species richness was identical, we compared the inflow intensity between the low elevational bands (band No. 1-13, from 2,350 to 3,650 m a.s.l.) and high elevational bands (band No. 14-26, from 3,650 to 4,950 m a.s.l.). We found that the mean of the inflow intensity of the low elevational bands (Means=842.85, Standard Deviation=94.75) was higher than the mean of the inflow intensity of the high elevational bands (Means=709.46, Standard Deviation=419.32) (t-test: $t = 1.12$, $P > 0.01$). Moreover, we also compared the “effective” species richness (defined as the number of species appearing in the “hump”) of the low abundance center species ($n=83$) and high abundance center species ($n=40$) to test the differences in inflow intensity. We found the elevational range of 77 species (93%) in low abundance center species overlapped with the “richness hump”, and the elevational range of 9 species (23%) of high abundance center species overlapped with the “richness hump” (Figure 2).

DISCUSSION

Species mean elevational range size pattern

Our study showed that the mean elevational range size pattern of breeding birds in Lebu Valley was a hump-shaped pattern. It is worth noting that there are several frequently used methods to describe species mean range size patterns. McCain (2013) used the “Steven’s method”, “midpoint method” and “quartile method” to explore the relationships of species mean range size and elevation for vertebrates from 160 mountains, and the results generated by these three methods vary greatly (McCain & Knight, 2013). For example, the result by using the Steven’s method showed that 40% of datasets found a positive relationship between species mean range size and elevation. However, only 0% and 38% of datasets found a positive relationship when using the midpoint method and the quartile method. Our study conducted three most commonly used methods to access the species mean elevational range size pattern, and all approaches yield a consistent hump-shaped pattern which indicated that our result was robust and unaffected by the measuring methods. However, to compare the results of different studies, we should use comparable methods to access the elevational range size pattern across regions or taxa.

Drivers of species mean elevational range size

In this study, we found the annual temperature range and normalized vegetation index were the most essential variables for species mean elevational range size, while the habitat heterogeneity had little influence on the species mean elevational range size. The annual temperature range was negatively correlated with species mean elevational range size, and normalized vegetation index was positively correlated with species mean elevational range size. These results indicated that the climate variability hypothesis, the ambient energy hypothesis, and the habitat heterogeneity hypothesis failed to predict the breeding birds’ mean elevational range size pattern in Lebu Valley.

The climate variability hypothesis

According to the climate variability hypothesis, the species range size expands as the stability of climatic conditions decreases (Stevens, 1989, 1992). Many studies have found evidence to support the climate variability hypothesis (latitude: Letcher & Harvey, 1994; Kockemann, Buschmann, & Leuschner, 2009; Morin & Lechowicz, 2013; Pintor, Lin, & Krockenberger, 2015; elevation: Pintor, Lin, & Krockenberger, 2015; Chan et al., 2016; Liang et al., 2020). Studies argued that this positive relationship was probably caused by the physiological tolerance of species (Kevin J. Gaston & Spicer, 2001). Species with wider physiological tolerances are generally considered to have a wider niche breadth, so the species can adapt to more habitats and thus have a wide range of distribution (Brown, 1984).

Our result was inconsistent with the prediction of the climate variability hypothesis (the annual temperature range was negatively correlated with species mean elevational range size along the elevational gradient in

Lebu Vally). There are many indicators to measure climate variability and using different indicators to access the climate variability hypothesis may lead to changes in the results. For example, seasonal temperature range was also considered as a good indicator of climate variability, and studies have shown that species range size could be positive correlated with seasonal temperature range (e.g., Kockemann, Buschmann, & Leuschner, 2009; Whitton, Purvis, Orme, & Olallatarraga, 2012; Chan et al., 2016; Liang et al., 2020). Hence, we correlated seasonal temperature range (additional to annual temperature range) with the species range size, and we also found that seasonal temperature range was negative correlated with species range size (standardized beta coefficient=-0.661, $R^2=0.436$, $P < 0.01$), which was also inconsistent with the prediction of climate variability hypothesis.

Climate variability is closely related to many other environmental factors (e.g., productivity, habitat). The influence of climate variability on species range size may have different manifestations under different situations (Letcher & Harvey, 1994). For example, the impact of unfavorable climate could be mediated by high productivity or resources. Moreover, climate variability also influences species range size in an evolutionary time (Kevin J Gaston, 1996). However, studies have struggled to take all these factors into account. Therefore, whether the climate variability hypothesis is applicable to explain the mean range size of species pattern (particularly regarding its generality when considering elevation) remains further tested in different regions and taxa.

The ambient energy hypothesis and the habitat heterogeneity hypothesis

The ambient energy hypothesis predicts that areas with high productivity can accommodate more species, and species interaction will be more frequent in the areas with high species richness, which could promote species specialization and lead to finer niche separation and smaller range size (Hildrew, Townsend, & Francis, 1984; Currie, 1991). However, to our knowledge, no empirical study found evidence to support the ambient energy hypothesis, whether along the latitude gradient or the elevational gradient. On the contrary, studies have shown positive or irrelevant relationships between primary productivity and species mean range size (e.g., Luo et al., 2011; J.-Y. Kim et al., 2019). In our case, we also detected a positive relationship between species mean range size and primary productivity.

Habitat heterogeneity also plays an important role in determining the species distribution (Whitton, Purvis, Orme, & Olallatarraga, 2012). Different combinations of habitat types can affect the energy allocation of an ecosystem. For example, higher habitat heterogeneity can promote the subdivision of limited resources (Kerr & Packer 1997). Therefore, the habitat heterogeneity hypothesis was proposed as a supplement to the ambient energy hypothesis (J.-Y. Kim et al., 2019). The habitat heterogeneity hypothesis indicates that complex habitats should facilitate the resource allocation in ecosystems, which could lead to greater species specialization and coexistence. Under certain conditions, an increase in available space and shelters, as well as opportunities for isolation and divergent adaptation, is thought to enhance species coexistence, persistence, and diversification (Rohde 1992). However, our results found little evidence to support the habitat heterogeneity hypothesis, and the area with higher habitat heterogeneity does not necessarily mean a larger area of suitable habitat. Our result showed that habitat heterogeneity was the lowest while the area percentage of suitable habitat types was the highest (Figure S3 in Appendix 2). The relationship between species mean range size and habitat heterogeneity in Lebu Valley may be weak in this case.

Non-directional rescue effect

The rescue effect emphasizes that the proximity of the range margins of potentially interacting species can impact species richness (Stevens, 1992). Our results detected a positive correlation between inflow intensity and species richness along the elevational gradient (Figure 4a), which indicated that the richness “hump” in the middle elevation of Lebu Valley should be “rescued” by the species from the lowland and highland simultaneously (non-directional rescue effect). Furthermore, the inflow intensity in the low elevations was higher than that in the high elevations, which indicated that the left-skewed species richness hump towards lower elevation in the Lebu Valley could be explained by the stronger inflow intensity in the low elevations.

Studies have shown that the hump-shaped pattern is one of the most common (about 50%) elevational

species richness patterns (Rahbek, 1995). Particularly, most of the recent studies on terrestrial vertebrates in the Himalayas have discovered a consistent hump-shaped elevational richness pattern across taxa (e.g., Acharya, Sanders, Vijayan, & Chettri, 2011; Ding et al., 2019; Hu et al., 2017; Pan et al., 2016; Joshi & Bhatt, 2015). However, studies are often fascinated by the relationship between environments (e.g., climate and productivity) and biodiversity, and few studies have explored another form of explanation for species richness pattern, such as species range size and the interaction between species richness and species range size. To better understanding the relationship between species richness and species range size, the rescue effect should be tested in more regions.

CONCLUSION

Our study showed that the pattern of the mean elevational range size of birds in Lebu Valley was a hump-shaped pattern, and species mean elevational range size negatively correlated with annual temperature range and positively correlated with the normalized vegetation index. While habitat heterogeneity was weakly correlated with species mean elevational range size. These results showed that all the hypotheses examined in our study (the climate variability hypothesis, the ambient energy hypothesis, and the habitat heterogeneity) failed to predict the elevational range size pattern of breeding birds in Lebu Valley. Given the uncertainty in species range size pattern, the generality of related hypotheses explaining the mean range size of species pattern remains to be further tested. Moreover, species inflow intensity could directly impact the species richness pattern in addition to the environmental factors. Our study provided new insights into the relationship between species richness pattern and species range size.

DATA AVAILABILITY STATEMENTThe data that support the findings of this study are available from Appendix 1.

COMPETING INTERESTS

The authors have declared that no competing interests exist.

AUTHOR CONTRIBUTIONS

Y.H. and S.C. conceived the idea for this study and designed the research; Y.H., S.C., and Z.Z. conducted the fieldwork; Y.H. and S.C. analyzed the data; S.C. led the writing with assistance from Singh, P. B., K.R., D.Z., and H.H. All authors contributed critically to the drafts and gave final approval for publication.

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TABLES

TABLE 1 The corrected Akaike’s information criterion (AICc) and the Goodness of Fit (R^2) of Polynomial regressions for mean elevational range size-elevation relationship (according to the Steven’s method, the midpoint method, and the specimen method).

		The Steven’s method	The midpoint method	The specimen method
AICc value	liner equation	336.31	390.73	380.71
	quadratic equation	311.53	362.60	369.02
	cubic equation	300.60	358.99	371.45
R^2	liner equation	0.41	0.05	0.02
	quadratic equation	0.80	0.71	0.44
	cubic equation	0.88	0.78	0.45

TABLE 2 Model selection for annual temperature range (ATR), normalized vegetation index (NDVI), and habitat heterogeneity (HH) of the breeding birds on Lebu Valley. The dependent variable was species mean elevational range size (according to the Steven’s method). “*” indicates the best models were evaluated using the corrected Akaike’s information criterion ($\Delta AICc < 2$).

Variables included in the model	R^2	AICc	Delta AICc	P	Std Beta Coeff.	Std Beta Coeff.	S
ATR+NDVI*	0.508	338.604	0	<.001	ATR	NDVI	H
ATR*	0.436	339.345	0.741	<.001	-0.414	/	/
NDVI*	0.416	340.278	1.674	<.001	-0.661	/	/
NDVI+HH+ATR	0.513	341.473	2.869	0.001	/	0.645	/
					-0.378	0.366	-

Variables included in the model	R ²	AICc	Delta AICc	P	Std Beta Coeff.	Std Beta Coeff.	S
NDVI+HH	0.446	341.714	3.110	0.001	/	0.589	-
ATR+HH	0.440	341.988	3.383	0.001	-0.628	/	-
HH	0.131	350.590	11.985	0.069	/	/	-







