

Ecological Traits Affect The Seasonal Migration Patterns Of Resident Birds Along A Subtropical Altitudinal Gradient

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Abstract

Background: Altitudinal bird migration involves seasonal shifts up and down the altitude gradient annually. Asia as the place with the largest number of altitudinal migrants, has quite few related studies, especially for montane and temperate avifaunas.

Method: To explore the potential drivers of seasonal altitudinal migration for birds in the middle of Hengduan Mountains, we conducted a two-year investigation on breeding and non-breeding season bird communities at eight altitude sections in the Gongga Mountains. Then, we examined the altitudinal migration patterns and relationships between seasonal distribution shifts and species' traits, of 20 species with sufficient data recorded in both seasons.

Results: We found that a large proportion of resident birds underwent altitudinal migration and showed 3 patterns (downslope shift, upslope shift, no shift). Species' seasonal distribution shifts were mainly correlated with territoriality, nest height, diet, and temperature tolerance range. The species nesting in scrub and omnivores were more likely to present a downhill movement in the non-breeding season. In addition, territorially weaker species migrated more widely and performed multiple patterns. Notably, HWI dominated upslope shifts in altitudinal migration.

Conclusion: Studying the seasonal altitudinal migration patterns of birds is essential to understanding their distributional responses to seasonal changes in climate (energy), which has important conservation implication for avian biodiversity. These results further consolidate the study of seasonal altitudinal migration in montane birds and verify that body mass is not correlated with altitudinal migration. This could be used to bridge existing knowledge gaps that currently impeding effective conservation.

Introduction

Understanding the variation of species distribution along altitudinal gradients over space and time is crucial to assess the impact of climate change on montane species [1]. The geological characteristics, physical and climatic conditions of mountains change rapidly with altitudes, and these changes can affect the distribution and abundance of species along the altitudinal gradient [2, 3]. Birds are often treated as important indicators that reflect the state of ecosystem functioning, because they are widely distributed, easy to detect and sensitive to environmental changes [4, 5]. They have played an important role in the mountain ecosystem, serving as arthropods predator, seeds consumer and disperser [6–8]. Their mobility has profoundly influenced many other aspects of their ecology and evolution, such as strong dispersal facilitates colonisation of new regions, thereby driving range expansion [9]. When on islands, speciation is most likely to occur when dispersal is relatively high [10], while on the mainland there is evidence that low dispersal promotes bird diversification [11]. Previous studies of avian movements have mostly focused on their migration (i.e. predictable, annually return movements between breeding and non-breeding ranges [12], and most species of avian migrants are partial migrants rather than complete migrants [13]. Such type of migratory behavior involves movements over altitudinal

gradients. Most birds conduct seasonal migrations over altitudinal gradients [12], including short-distance upslope movement from low-altitude breeding areas to high-altitude non-breeding areas and downslope movement from high-altitude breeding areas to low-altitude non-breeding areas [5, 12, 14, 15]. Compared with latitudinal migrations, altitudinal migration is characterized with shorter distances such that individuals consume less energy.

Asia is home to the greatest number of altitudinal migrants of the world and it is estimated that up to 65% of the Himalayan and 58% of Taiwanese high-elevation breeding species are involved in this activity [12, 16]. However, this behaviour remains poorly understood, especially for montane and temperate avifaunas. Studying the seasonal altitudinal migration patterns of birds is essential to understanding their distributional responses to seasonal changes in climate (energy), which has important conservation implication for avian biodiversity [6, 15].

According to previous research, birds can reduce risk of predation [17], avoid the harsh climatic conditions [18, 19] and track the food resources by vertical migration [20–24]. Species with different life-history and ecological traits also show different migration patterns in response to climate change and several related ecological traits such as territoriality [25], nest height [17, 26], diet [27] and body mass [28] that could influence species' ability to shift their altitudinal ranges [28, 29]. Most studies on altitudinal migration have focused on the food-limitation hypothesis, which proposes that food availability varies seasonally over altitudinal gradients in response to fluctuations in temperature and precipitation throughout the year [15]. Animals may move up and down in altitudes in response to these variations. Consequently, species with different diets may respond differently to seasonality. For example, in some regions, frugivores and nectarivores are more likely to exhibit altitudinal migration than omnivores and invertivores [16, 20, 21, 23]. Similarly, avian territorial behaviors may also influence their distributional responses to climate change because species with stronger territoriality may guard the territory year-round [25, 30]. In addition, birds may actively adopt strategies to avoid or reduce nest predation. A probably more noticeable strategy is nest-site selection, which often determines the safety of the nest [26, 31]. It can be expected that species with lower nest sites have greater probability of altitudinal migration than species with higher ones. However, while many possible drivers of seasonal altitude migration have been proposed, they have only been empirically examined in few cases and their generalizability is mostly unknown [12, 32].

The causes of altitudinal migration have only been studied in a few systems and species. Most studies have been conducted in America, with few studies located in Asia [15]. Boyle found that altitudinal migration was prevalent, occurring in >20% of continental North American and nearly 30% of Hawaiian species [12]. In addition, majority of birds that undergo altitudinal migration are frugivores or nectarivores in the Neotropics [17, 33, 34]. In China, Taiwanese scholars modeled the behavior based on occurrence records collected by citizen scientists and suggested that seasonal variations in climates and food availability could be major drivers of the behavior [16]. Studies in the Gaoligong Mountains have found that species' seasonal distribution shifts were mainly associated with breeding altitudes and diet [23]. Relative to long-distance latitudinal migration, altitudinal migration has been poorly studied in Asia. More

studies testing altitudinal migration drivers in various regions is needed to provide a more complete view of the trade-offs associated with different migratory strategies in a diversity of taxa and ecological contexts.

As one of the world's 36 biodiversity hotspots, the Hengduan Mountains is rich in species diversity and endemism [35–38]. Local unique biogeographic (at the junction of Palaearctic and Oriental realm) and climatic features have drawn scientists' attention to biodiversity of the area. [39–41]. To explore the potential drivers of seasonal altitudinal migration for birds in the middle of Hengduan Mountains, we conducted a two-year investigation on breeding and non-breeding season bird communities at eight altitude sections in the Gongga Mountains, and compared species' altitude ranges between the two seasons. Our aims were to explore (1) the altitudinal migration patterns of mountain resident birds and (2) what life-history and ecological characters of birds are the primary drivers of seasonal altitudinal changes? Specifically, we predicted that insectivores and species with lower nest sites are more likely to conducted altitudinal migration. Further, species with a wider temperature-adapted range might have more pronounced changes in altitudinal distributions from the breeding to the non-breeding season, because they are more adaptable and have a wider ecological niche [16, 42].

Materials And Methods

Study area and field surveys

Mt. Gongga is located at the southeastern margin of the Qinghai-Tibet Plateau (29°20'-30°39'N, 101°30'-102°12'E, Fig. 1), the middle part of Hengduan Mountains, the middle part of Daxue Mountain and the western part of Sichuan. The main peak of Mt. Gongga is 7556 m above sea level. The region is at the transitional climatic zone of the warm and humid subtropical monsoon climate of eastern China and semi-humid climate of the eastern Qinghai-Tibet Plateau. Due to the large altitudinal coverage, the heat and moisture conditions vary with altitudes and the climate at the foot of the mountain is dry and warm [43]. With rising altitudes, the average annual precipitation of areas at 3000 m can reach 1930 mm, making the Gongga Mountain develop a complete montane vertical spectrum from subtropical to alpine frigid zone. Vegetation types and soils here also show obvious vertical differentiation [4, 8].

From May 2017 to December 2018, We conducted avian community surveys in the Hailuoguo region along the altitudinal gradients using standard line-transects during the breeding and non-breeding seasons. We divided the altitudinal gradients into eight sections at an interval of 400m, with the bird surveys spanning the entire set of all sections [6]. Our actual survey covered the altitudes from 1200 m (with the Dadu River as the lower altitudinal limit) to 4200 m above which is the permafrost. We conducted four surveys from 2017 to 2018, with each year consisted of two sampling seasons (i.e. breeding and non-breeding seasons). To ensure comparable efforts, the lengths of the transects in two seasons were similar within the same altitudinal section, which were approximately 2–3 km. Our team was composed of 2–3 well-trained personnel and the bird survey was conducted four times a day: every 30 minutes between dawn and morning (6:00–9:30) and between afternoon and sunset (15:30 – 18:30),

and in each time period an uphill and a downhill survey were performed. By doing so, we ensured that more bird species could be observed. For each survey, we recorded vegetation types, bird occurrences and abundances, and the information on birds' locations using a handheld GPS.

We recorded a total of 161 bird species in the two-year survey, and then quantified the change in the altitudinal range for each species between breeding and non-breeding seasons. First, by screening the residence type and distribution records, we excluded migratory birds that only breed in the area or spend the winter [44]. Second, we excluded highly aerial species and rare birds in small numbers, including swifts, raptors and pheasants. The reason is due to the inaccurate estimation of birds elevational ranges, as the elevation differences between observed subjects and researchers exist [4, 7, 23]. Finally, for comparison purpose, we focused on species that were recorded in both seasons. To improve the credibility only the species that were recorded in two altitudinal sections and above, and with more than five individuals in each season were used to study species' seasonal range shifts. These treatments resulted in a sum of 20 species for further analyses.

Before comparison analysis, we controlled for the potential difference in potential sampling efforts between the two seasons (the uneven samples may result in the distribution of bird observations biased towards the altitudes surveyed more often). A resampling approach was applied to standardize the sampling efforts. We examined the shifts in upper range limit, lower range limit and abundance-weighted range centre of the 20 species. The abundance-weighted range centre of each period was calculated as:

$$\sum_{m, n} E_i \times P_{Ai}$$

where m and n were the range limits of species A , E_i was the altitude (m) of site i and P_{Ai} was the proportion of species A individuals at site i in its total individuals recorded along the whole gradient [45].

To standardize the sampling effort, we randomly resampled (100 times without replacement) each altitudinal section datasets to generate the identical number of individuals between altitudinal section at each period (e.g. 1200 m, with 83 individuals in the breeding season and 283 individuals in the non-breeding season) [46, 47], in the R environment (version 3.6.4). Then we compared the average values derived from 100 random resamplings of the two periods to assess the range shift pattern for each of the three altitudinal locations (i.e. upper range limit, lower range limit and abundance-weighted range centre).

Assessment the association between seasonal distribution shifts and species traits

We examined the effects of species' traits on their altitudinal range shift patterns. The selected traits included flight efficiency, territoriality, average annual mean temperature of breeding/resident range (annualtemp), average temperature seasonality of breeding/resident range (temprange), nest height, diet and body mass. we obtained species' territoriality from the Tobias' dataset (categorical: strong and weak) [25]. We extracted the information on handwing index from another research [30]. Hand-wing index is a

proxy of avian flight efficiency and dispersal ability that measured by the ratio of Kipp's distance (the distance between the tip of the longest primary feather and the tip of the first secondary feather) to the wing chord. Based on WorldClim v1 database [48], we divided the temperature index into annualtemp and temprange, which more accurately represent an individual's tolerance criteria for suitable temperature. Finally, we obtained nest site (shrub, canopy), body mass and diet (invertebrates, omnivore) data from the dataset on the life-history and ecological traits of Chinese birds [49]. The body mass has received equivocal support in altitudinal migration studies. Although body mass is traditionally used as an index for dispersal ability in vertebrates, with larger size assumed to indicate greater dispersal ability [50]. However, in a recent study on bird dispersal ability (HWI), body mass did not correlate significantly with it [48]. Accordingly, we chose to keep the body mass as a candidate factor. Seasonal fluctuation of food resources is considered to be one of the major drivers of avian migration. Animals may move up and down in elevation in response to these variations.

We constructed the phylogenetic generalized least squares regression models (PGLS) in packages 'caper' [51] to examine the correlations between the shifting patterns in three altitudinal locations of species and their traits. To obtain the phylogenetic information, we downloaded 5000 phylogenetic trees of 20 target species from birdtree.org [52] and constructed the Maximum Clade Credibility tree using mean node heights with the software TreeAnnotator v1.10.4 of the BEAST package [53, 54]. We constructed three separate PGLS models for these three measures of altitudinal shifts. In the first model, the upper-elevation limit shift was the response variable. Territoriality, flight efficiency, temperature indexes, nest site, diet and body mass were used as predictors. Then we constructed two other models with the same prediction factors, using the lower-altitude limit and the abundance-weighted range centre shifts as response variables. All statistical analyses were conducted using the R statistical computing environment v.3.6.4 [55]. PGLS models were built as implemented in the package 'nlme' [56]. All phylogenetic paired t-tests used the 'phyl.pairedttest' function of the 'phytools' package in R [57].

Results

Seasonal range shift patterns

Our results revealed that a large proportion of resident bird species conducted seasonal altitudinal range shifts in Mt. Gongga. However, diverse patterns were performed. All 20 species showed seasonal shifts in their abundance-weighted range centre and altitude limits. Among them, the altitudinal difference of 14 species were below zero, indicating downhill migration from breeding to non-breeding season, while the other 6 species were above zero, indicating uphill migration. There were three altitudinal shift patterns among the studied species (Fig. 3). First, most species (11) bred at a higher altitude in breeding season, while migrated downward in non-breeding season. Second, some species (2) tended to move higher in non-breeding seasons, as both their abundance-weighted range centres and upper-altitude limits showed upward movements (Fig. 3). At last, the altitudinal ranges of seven species did not change significantly between seasons, and the altitudes during the breeding and non-breeding seasons were

mostly the same (the abundance-weighted range center altitude change $< 50\text{m}$), suggesting that the partial migration might be prevalent among the migrants (Fig. 2).

Effects of species' traits on shift patterns

The PGLS models indicated that HWI, nest height, annual temp and temprange (Table 1) were important in explaining the elevational shifts from breeding to non-breeding seasons (Fig. 2). In the uphill-altitude model, annual temp was positively correlated with upslope shift, while temprange was negatively correlated with upslope shift. Temperature changes were closely related to seasonal altitude shifts, as confirmed by our model results. Both the lower-altitude limit and the abundance-weighted range center shift model indicated that the species nesting in scrub were more likely to present a downhill movement in the non-breeding season. Moreover, we found that seasonal shifts were associated with flight efficiency, for the range of both uphill movement and abundance-weighted range center changes were positively correlated with HWI.

Phylogenetic paired t-test showed that territoriality, nest height and diet were significantly correlated with altitudinal shifts (Table 2). Specifically, territorially weaker species migrated more widely and had even diverse patterns than stronger species. For species with different diets, omnivores showed apparent downslope shifts in weighted mean altitude in the non-breeding season. For nest height, shown by the PGLS results, scrub-nesting species had a broader range of migration and presented a downward shift in the non-breeding season. No correlation was found between other traits in our models.

Table 1

Parameters	Estimate	SE	Z value	Pr(> z)
Lower-altitude limit shift				
HWI	32.825	13.043	2.517	0.021
Territoriality(Strong versus Weak)	400.000	234.500	1.706	0.105
AnnualTemp	2.305	19.956	0.116	0.909
TempRange	25.188	22.128	1.383	0.270
Nest Height(Canopy versus Scrub)	533.330	184.680	2.888	0.010
Diet(Insectivores versus Omnivores)	-2.250	2.684	-0.838	0.413
Bodymass	2.305	19.956	0.116	0.909
Upper-altitude limit Shift				
HWI	-9.949	11.068	-0.899	0.381
Territoriality(Strong versus Weak)	-2.667	1.778	-1.500	0.151
AnnualTemp	29.392	13.184	2.229	0.039
TempRange	-33.428	15.168	-2.2039	0.041
Nest Height(Canopy versus Scrub)	2.015	1.667	0.000	1.000
Diet(Insectivores versus Omnivores)	2.301	2.041	0.000	1.000
Bodymass	-52.167	155.165	-0.3362	0.741
Abundance-weighted Mean Altitude Shift				
HWI	25.932	8.454	3.068	0.007
Territoriality(Strong versus Weak)	218.090	166.090	1.313	0.206
AnnualTemp	16.246	13.188	1.232	0.234
TempRange	-5.945	15.698	-0.379	0.709
Nest Height(Canopy versus Scrub)	242.820	142.620	1.703	0.106
Diet(Insectivores versus Omnivores)	-41.793	187.956	-0.222	0.827
Bodymass	48.641	143.061	0.340	0.738

For each measure of the altitudinal shifts (the lower-altitude limit shift, the abundance-weighted mean altitude shift, the upper-altitude limit shift), we used a phylogenetic generalized least-squares (PGLS) model, with HWI, Territoriality, AnnualTemp, TempRange, Nest Height, Diet and Bodymass as predictors.

Territoriality of both strong and weak. Diet groups included insectivore and omnivore. Nest Height has a focus on nesting in Canopy and Scrub.

Table 2

Trait groups	Altitude shifts	N	t	df	P
Territoriality					
Strong	Upper-altitude limit	0.009	2	0994	
	Lower-altitude limit	5	1.829	2	0.209
	Mean altitude	5	3.006	2	0.095
Weak	Upper-altitude limit	2.982	0.011		
	Lower-altitude limit	15	-0.200	12	0.844
	Mean altitude	15	1.898	12	0.819
Nest Height					
Canopy	Upper-altitude limit	12	2.697	9	0.245
	Lower-altitude limit	12	-0.437	9	0.672
	Mean altitude	12	1.165	9	0.274
Scrub	Upper-altitude limit	1.611	5	0.168	
	Lower-altitude limit	8	2.727	5	0.041
	Mean altitude	8	4.261	5	0.008
Diet					
Insectivores	Upper-altitude limit	4	2.010	1	0.294
	Mean altitude	4	1.413	1	0.692
Omnivores	Upper-altitude limit	16	2.149	13	0.051
	Lower-altitude limit	16	1.775	13	0.099
	Mean altitude	16	2.593	13	0.022

For each trait group, we used the phylogenetic paired t test to compare the altitudinal distributions between breeding and non-breeding seasons. Significant differences are marked in bold (95% CI of shifts do not overlap with zero). The mean elevation was abundance-weighted.

Discussion

We described the patterns and driving factors of vertical migration for resident birds in Mt. Gongga through four surveys in two years. Consistent with previous studies in Europe and North America [12, 15, 16, 23, 27], our results show that altitudinal migration is common in resident birds, and seasonal change in temperature, food availability and fecundity may be the main driving factors for the altitude migration. Most resident birds migrate downhill after breeding season at high altitudes, while some species migrate upward and downhill in non-breeding season. Migration not only exists in migratory birds, but also in resident birds. Under the influence of climate change and human activities, montane species are facing unique challenges such as habitat fragmentation.

We found that compared to insectivores, omnivores have greater range of altitudinal migrations and exhibit multiple shifting patterns in Mt. Gongga (Table 2). Insectivores in our study did not perform uphill movement during the breeding season and tended to shift their distribution boundaries downhill during non-breeding season, which is probably correlated with the distributions of invertebrates [16, 23]. In mountainous areas, invertebrate abundance normally decreases from birds' breeding to non-breeding season, [58–60], and this decline is particularly obvious at high altitudes. In breeding season the invertebrate resources at the altitude inhabited by insectivores are sufficient to meet their needs, but harsh climates and reduced food supplies over non-breeding season may drive them to move downhill [19, 23, 27]. The demand for various food types at different periods in a year may also drive altitudinal movements. A more diverse diet spectrum allows omnivores to use habitats at different altitudes and thus perform altitudinal migrations to obtain food resources, thus presenting varying migration patterns.

Our results show that the weakly territorial species had more diverse migration patterns, and strong territoriality species tended to move uphill (Table 2). Researchers generally accepted the idea that strong territorial species would expend more time defending their territories [25, 30], so that they are less likely to go through rapid distribution changes but may be constrained to move upwards by interactions with closely related species [61, 62], whereas species with weak territoriality would continuously move to seek access to food resources [25, 63]. Changes in temperature have great impact on bird's behaviour, as we found that species with a narrower temperature range ($< 30^{\circ}$) migrate predominantly uphill during the breeding season, and species with a wider temperature range ($> 30^{\circ}$) and lower annual temperature ($< 10^{\circ}$) tend to migrate downhill during the non-breeding season (Table 2). This is consistent with the results of another research carried out in Taiwan [16]. Species with wider range of temperature tolerance and cold endurance will have greater opportunities to broaden their ecological niches in competition as predicted. Meanwhile, relying on the rich food resource in Gongga and better cold endurance allow them to breed at higher altitudes, to avoid the more intense resource competitions at lower altitudes [16]. In addition, nearly all 8 species with wider temperature range ($> 30^{\circ}$) and lower annual temperature ($< 10^{\circ}$) are weakly territorial species except *Trochalopteron elliotii*, verifying our conjecture that species with weak territoriality will put more effort in foraging resources. If temperature changes intensify interspecific competition, those species would be forced to migrate at altitudes for an 'exploration', and adjust to colder and harsher conditions for breeding season.

The relationship between nest structure and nest predation is controversial [64], and the nest predation risk is not necessarily higher at lower elevations [34]. Our results show that migratory movements are associated with predation risk, with scrub-nesting birds migrating downslope and moving more widely on average than canopy-nesting birds, which we suggest is related to the type of vegetation in different seasons (Table 2,3). Nest height often determines the safety of a nest as a strategy to avoid nest predation or maladaptation [26, 31]. And the nest predation rates could generally be reduced by the increase of height-related coverage and complexity of vegetation surrounding the nest. (Holway 1991; Martin 1993; Arriero et al. 2006; Hollander et al. 2015; Buehler et al. 2017; Bellamy et al. 2018; Haohui Guan, 2018). In non-breeding season when dead scrub increases the predation risk and the negative effects of extreme conditions for both exposed nests and individuals [12], choosing to move downhill to find more suitable habitat increases the chances of survival. Canopy-nesting birds rarely conduct elevational migration, which is probably because their nest sites are higher and less exposed in the montane habitats of mixed coniferous or deciduous forests, thus reducing the predation risk.

When considering the absolute speed of shifts (ignoring shift direction) as well as expansions in species' upper limits, the most important predictor was HWI [28, 30]. Our modelled results show a correlation between HWI and uphill movement (Table 2), which is not difficult to understand that the uphill movement consumes more energy in the mountain system. Dispersal distances increase exponentially with flight efficiency in resident birds of Mt. Gongga [48]. Flight efficiency and migratory behaviour are strongly and consistently associated with variation in dispersal distances, which is consistent with the idea that the energetic cost of transport is a major determinant of dispersal distances [65]. Moreover, the possibility of estimating dispersal ability based on morphology may have applications in conservation biology, as this can be instrumental in assessing species vulnerability to habitat fragmentation and climate change [66]. However, due to our small sample size, it is impossible to make a more detailed analysis with the height and migration rate of HWI.

Body mass is not associated with seasonal shifts in altitudes, which is consistent with a recent study in Gaoligong [23]. Most of the studies on the correlation between body mass and altitude migration were conducted in tropical and smaller altitude span regions [16, 28]. Claramunt also found that body mass was not important in explaining prenatal dispersal distances in British birds, and that the correlation between the two was low and not statistically significant [48, 67]. Second, there was no significant difference in body mass among our respondents and the relationship between transport and body mass in birds has been attributed to variation in wing shape, in which larger birds have also higher aspect ratios, rather than an intrinsic effect of body mass itself [68, 69]. Body mass has long been linked to environmental gradients by Bergmann's rule [70], which states that larger-bodied species tend to be found in colder environments. However, evidence for the existence of Bergmann's rule is variable [71–73], and it tend to be applied more to intraspecific variation in body mass or variation among closely related species, particularly along latitudinal gradients.

Conclusions

Altitudinal migration has evolved independently in different regions of the world under the different environmental pressures coupled with varying life history characteristics. These external drivers frequently interact with intrinsic factors such as seasonality of requirements due to reproduction, differences in individual condition, and competitive asymmetries among individuals to produce flexible partial migration systems. Additionally, the prevalence of partial migration implies that a combination of intrinsic and extrinsic drivers commonly shape migratory decisions at the individual level. Investigations of partial altitudinal migration patterns that focus on underlying mechanisms that lead to different individual responses to environmental factors could help elucidate how individual characteristics affect migratory propensity. Our results showed that some resident birds undertook seasonal altitudinal migration and had three patterns: downslope shift, upslope shift and no shift. Six main drivers influencing seasonal altitudinal migration of birds in the region include territoriality, nest height, HWI, annualtemp, temprange and diet, and we further determined body mass did not correlate with transport of birds. Our study not only consolidates the findings of others, but also expanding understanding of the fitness trade-offs between migration strategies and how they are reflected in the population dynamics of montane species.

Declarations

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Availability of supporting data

The morphological and ecological data used in this study is available at <https://www.nature.com/articles/s41467-020-16313-6> and <https://www.biodiversity-science.net/CN/10.17520/biods.2021201> .

Range information and migration data is publicly available from www.birdlife.org ; climate data from www.worldclim.org ; phylogenetic data from www.birdtree.org .

Conflict of Interest

The authors declare no conflicts of interest.

Authors' Contributions

Yuwen Cheng , Zhixin Wen, Xingcheng He and Yongjie Wu conceived and designed the study. Yuwen Cheng, Xingcheng He, Zhehan Dong, Mingyu Zhangshang, Dongrui Li and Yan Wang performed the field surveys and analysed the data. Yuwen Cheng, Zhixin Wen, Xingcheng He and Yongjie Wu wrote the manuscript.

Ethical Approval and Consent to participate

Not applicable.

Consent For Publication

Not applicable.

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Figures

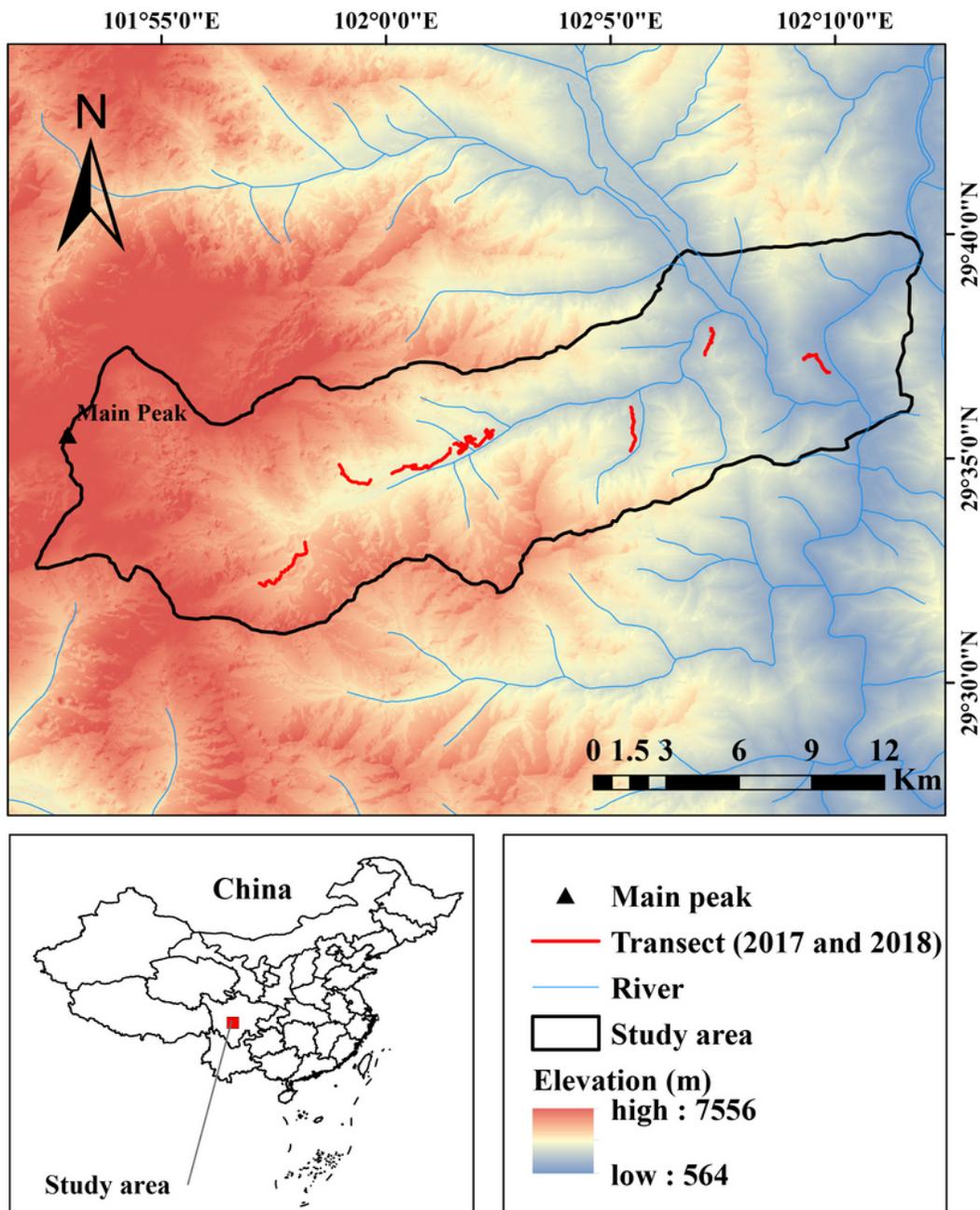


Figure 1

Location of study, invertebrate sampling sites, and bird survey transects. The study area was separated into 8 sampling altitudinal sections (from 1100 to 4400 m). Bird survey transects are indicated by red lines for 2017 and 2018.

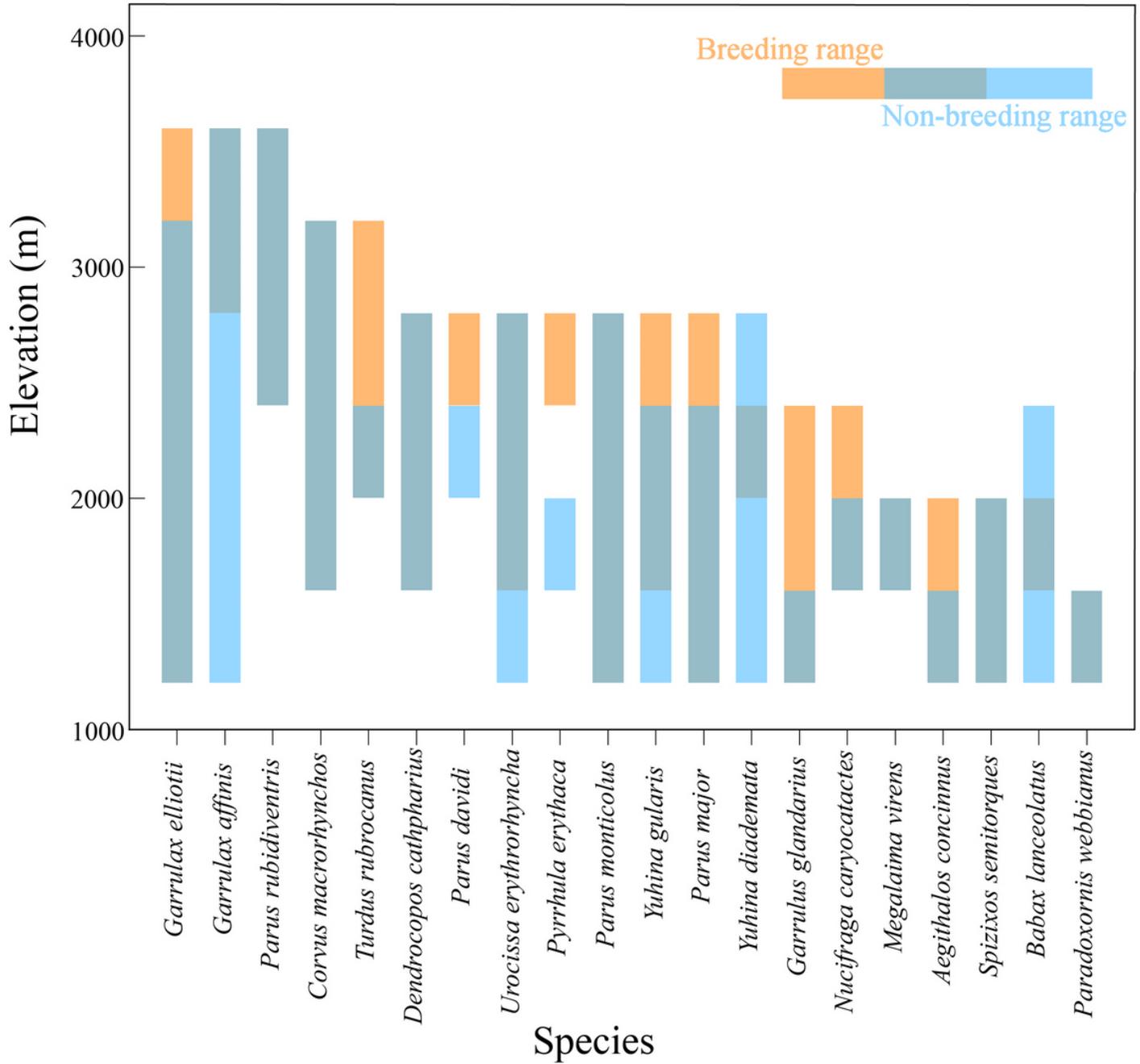


Figure 2

Species-level seasonal shifts in altitudinal ranges along the altitude gradient in the Gongga Mountains in southwest China. For each species, orange and blue bars indicate the altitudinal ranges in the breeding and non-breeding seasons, respectively, and the overlap between the bars indicates the range where the species was recorded in both seasons. Species in the x-axis were ordered with decreasing abundance-weighted mean altitudes.

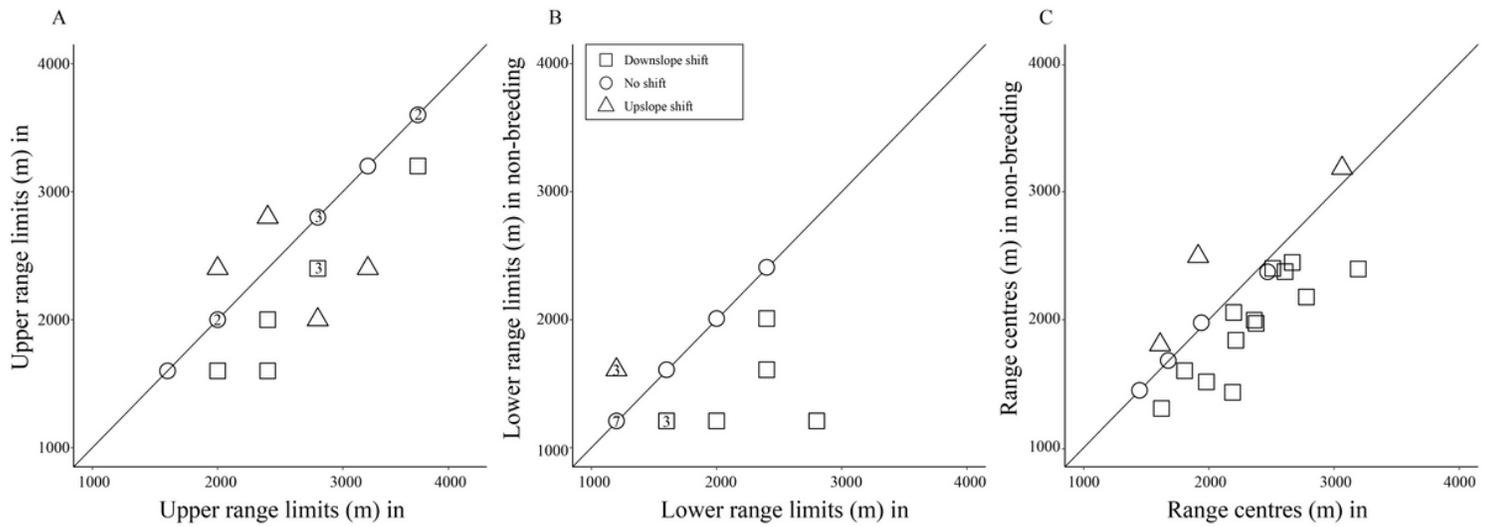


Figure 3

Altitudinal shifts of A upper range limits, B lower range limits and C abundance-weighted range centres of 20 species between breeding and non-breeding seasons. Values inside graphs represent the number of species showing the same range dynamics over time.

Supplementary Files

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