Seasonal variation in community composition and distributional ranges of birds along a subtropical elevation gradient in China

Dan Liang1,2,3 | Xinyuan Pan1 | Xu Luo2 | Cheng Wenda4 | Yanyan Zhao1 | Yiming Hu5 | Scott K. Robinson6 | Yang Liu1

Abstract

Aim: Seasonal variation in community composition and species distributional ranges along elevational gradients remain poorly known but are essential to inform conservation. In this study, we aim to understand how species richness, community composition and elevational ranges of montane birds change between the breeding and the non-breeding season.

Location: The east slope of the southern Gaoligong Mountains, Yunnan, southwest China, elevational range: 700–3,400 m a.s.l.; latitudinal range: 24°56′–26°09′N.

Methods: We compared species richness and community composition of birds in nine 300-m elevational bands in the breeding (April–May) and non-breeding (December–January) seasons. We also calculated seasonal elevational shifts of 97 species with sufficient data recorded in both seasons and assessed how species’ traits influenced these shifts.

Results: Species richness declined in high and low elevations between the breeding and the non-breeding season. The temporal beta diversity shift from the breeding to the non-breeding season was mainly caused by species losses rather than species gains in high- and low-elevation communities. Communities in middle elevations showed a contrasting pattern, with seasonal composition change resulting mainly from species gains. We also found that species’ seasonal distribution shifts were mainly associated with breeding elevation and diet. Notably, high- and middle-elevation breeders and insectivores significantly shifted their elevational ranges downslope in the non-breeding season. In addition, species that participate in mixed-species flocks and that rely on forests also showed significant downslope shifts in the non-breeding season.

Main conclusions: These results show complex patterns of the interconnectedness of bird communities along the elevational gradient. Keeping forests at middle elevations intact appears especially important as they are used in winter by species that breed at both high and middle elevations. Furthermore, our results suggested conservation actions maintaining connectedness in low and middle elevations are urgently
Species with different traits respond to seasonal variability in environmental conditions differently; therefore, it is vital to evaluate how traits affect interspecific variation in seasonal distribution shifts (Hsiung et al., 2018; Tsai et al., 2021). Some traits may predispose species to shift their distributions seasonally. Species that breed in higher elevations may show significant seasonal downslope movements, whereas some lower-elevation breeding birds showed significant upslope movements in winter (Tsai et al., 2021). Such interspecific variation in elevational shifts may correlate with diet, in which species with different diets may respond to seasonality differently as food resources vary across seasons. Diet effects on temporal distribution shifts might be region- and scale-specific. Whereas on a global scale, insectivores tend to be seasonal elevational migrants (Barçante et al., 2017), they tend to move less in tropical mountains of south-eastern Peru (Merkord, 2010). Other species’ traits have also been associated with seasonal shifts in elevation. For instance, smaller species may shift to lower elevations (Tsai et al., 2021), and species that rely on forests and species that participate in mixed-species flocks have also shown significant temporal elevation shifts (Elsen et al., 2017; Merkord, 2010; Zhang et al., 2020).

The Himalayan–Hengduan Mountains are among the most mountainous regions in the world and are global biodiversity hotspots (Myers et al., 2000; Wu et al., 2013). Previous studies showed that bird species richness in these regions reaches a peak in the middle elevations, and this pattern is driven by extreme climate conditions at high elevations and high human disturbance in low elevations (Pan et al., 2016, 2019; Wu et al., 2013). However, these studies focused on spatial patterns of bird diversity, and we know little about the seasonal elevational movements of species in these regions (Barçante et al., 2017; Hsiung et al., 2018). Elevational migrants account for a large proportion of species composition in this region, including songbird groups such as thrushes, babblers, flycatchers, warblers and finches (Liu & Chen, 2021). Furthermore, most of these songbirds are forest dwellers and thus may be sensitive to land-use change in their non-breeding habitats. Hence, elevational migrants may face different challenges in different annual stages; accounting for seasonal elevation shifts may improve the effectiveness of conservation efforts (Elsen et al., 2018; Wu et al., 2010).

Here, we surveyed bird communities in nine elevational bands of the Gaoligong Mountains in the breeding and non-breeding seasons and compared the species composition of each elevational band and species’ range shifts between two seasons. We addressed two questions. First, how do species diversity and community composition change between breeding and non-breeding seasons? We predicted a significant shift in community composition at high elevations with...
harsh environmental conditions during the non-breeding season and, potentially, at middle and lower elevations, as species bred in forests at middle elevations might move into the lowland, agriculture landscapes. Second, which traits can predict the seasonal elevation shifts of species between seasons? We predicted that species that breed at higher elevations and those with more specialized diets such as insectivores might have more significant changes in elevation distributions from the breeding to the non-breeding season. We also expected smaller-bodied species, species that rely on forests, and those that participate in mixed-species flocks would be most likely to show downslope movements in the non-breeding season.

2 | METHODS

2.1 Study sites and community surveys

Our research sites were located on the east slope of the Gaoligong Mountains in southwest China (24°55′–26°31′N, 98°41′–98°53′E) (Figure 1a), a subtropical biodiversity hotspot that harbours rich bird diversity with high endemism (Dumbacher et al., 2011). This area is characterized by substantial spatial and seasonal changes in climatic conditions; temperature and precipitation vary across elevation and between wet and dry seasons (Pan et al., 2019; Xue, 1995). As with most of the mountains in southwest China, human settlements and other anthropogenic habitats such as croplands dominate the lowlands (concentrated in 700–1,600 m a.s.l.) of the Gaoligong Mountains (Figure 1b). In contrast, nature reserves protect habitats of middle-to-high elevations against human disturbances (Pan et al., 2019; Wu et al., 2013; Xue, 1995).

From April 2016 to December 2020, we conducted avian community surveys using standard line transects (Bibby et al., 2000) along the elevational gradient in breeding and non-breeding seasons. We divided nine 300-m elevational bands from 700 m a.s.l. (around the lowest elevation in Salween valley) to 3,400 m a.s.l. (the mountain peak), a cut-off that has been used in studying the species richness pattern of birds in this region (Hu et al., 2018; Pan et al., 2016, 2019). The lowest three elevational bands (700–1,600 m a.s.l.) were dominated by anthropogenic habitats such as croplands. The four middle-elevational bands (1,600–2,800 m a.s.l.) were covered mainly by forests, and the two highest elevational bands (2,800–3,400 m a.s.l.) consisted of shrublands such as rhododendrons and bamboo at or above treeline. For each elevational band, we located two to four transects varying in length, with the total lengths of transects in each elevational band were approximately seven km to ensure comparable efforts (Table 1; Figure 1). For the breeding seasons between 2016 and 2019, we conducted our surveys eight times in all transects in April and May (i.e. two replicates per year) when birds were actively breeding (Liang et al., 2017, 2018; Pan et al., 2019). We conducted non-breeding surveys along the same transects in two non-breeding seasons from December 2018 to January 2019 and in December 2020. Despite the unbalanced sampling years among the two seasons (the breeding survey was conducted in four seasons, whereas the non-breeding survey was only conducted in two seasons), we had the same sampling effort (eight replicates) and similar sampling coverage for each elevational band in two seasons (Table 1). We only surveyed when birds were
### Table 1: Seasonal changes in bird richness and composition at nine elevational bands in the Gaoligong Mountains in southwest China

| Elevational band (m) | Number of Transects | Lengths of Transects (km) | Observed Richness (Breeding) / Sampling coverage | Observed Richness (non-breeding) / Sampling coverage | Mean Estimated Richness (Breeding) (2.5%–97.5% CI) | Mean Estimated Richness (non-breeding) (2.5%–97.5% CI) | Temporal beta diversity Index (TBI) | Species Losses (B) | Species Gain (C) | pTBI |
|----------------------|---------------------|---------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------|-----------------|-----------------|------|
| 700–1,000            | 4                   | 7.05                      | 104/0.981                                     | 81/0.970                                      | 128 (113–166)                                 | 128 (99–177)                                  | 0.398                             | 0.248           | 0.150           | 0.297 |
| 1,000–1,300          | 3                   | 7.29                      | 93/0.973                                      | 89/0.973                                      | 115 (101–152)                                 | 98 (91–116)                                   | 0.381                             | 0.195           | 0.186           | 0.514 |
| 1,300–1,600          | 2                   | 7.5                       | 124/0.939                                     | 134/0.975                                     | 153 (137–188)                                 | 151 (141–176)                                 | 0.298                             | 0.165           | 0.134           | 0.996 |
| 1,600–1,900          | 3                   | 7                         | 127/0.982                                     | 133/0.980                                     | 150 (136–185)                                 | 160 (144–197)                                 | 0.325                             | 0.162           | 0.162           | 0.964 |
| 1,900–2,200          | 2                   | 7.2                       | 91/0.928                                      | 96/0.965                                      | 123 (105–166)                                 | 136 (114–196)                                 | 0.416                             | 0.205           | 0.210           | 0.157 |
| 2,200–2,500          | 3                   | 7.3                       | 102/0.939                                     | 107/0.974                                     | 131 (114–169)                                 | 137 (119–180)                                 | 0.349                             | 0.161           | 0.188           | 0.839 |
| 2,500–2,800          | 2                   | 7                         | 85/0.949                                      | 78/0.977                                      | 101 (91–130)                                  | 100 (85–140)                                  | 0.380                             | 0.205           | 0.175           | 0.511 |
| 2,800–3,100          | 2                   | 7.18                      | 80/0.960                                      | 40/0.977                                      | 98 (87–128)                                   | 54 (47–78)                                    | 0.455                             | 0.315           | 0.139           | 0.021 |
| 3,100–3,400          | 3                   | 7.08                      | 55/0.940                                      | 26/0.965                                      | 81 (63–104)                                   | 30 (29–45)                                    | 0.660                             | 0.462           | 0.198           | <0.001 |

Note: The mean estimated richness for each elevational band in each season was calculated as the estimated asymptotic richness using the sample-sized-based rarefaction and extrapolation (R/E) sampling curves with Hill number ($q = 0$). We selected two replicates in each of the two breeding seasons in 2018 and 2019, and two random replicates in each of the two non-breeding seasons in 2019 and 2020. See Table S1 for the sensitivity of the estimated species richness using different combinations of replicates in two different years in both seasons. Temporal beta diversity index (TBI) in this study measured change in species composition between the breeding and the non-breeding season and was then decomposed into species losses (B) and gains (C). The significant change in community composition between two seasons is marked in bold.
showed a unimodal distribution along elevation; hence, we included sampling across a large elevational range and many of our bird data. Ability could change between seasons but not among elevations. Our ability to determine whether a species occupies an elevational band, while detection probability in each elevational band in each season with temporal replicates (different surveys). We assumed both elevation and season (i.e. elevation, elevation^2, elevation*season, season) could affect whether a species occupies an elevational band, while detection probability could change between seasons but not among elevations. Our sampling covered a large elevational range and many of our bird data showed a unimodal distribution along elevation; hence, we included quadratic terms in our model (Moritz et al., 2008). Thus, we have 14 competing models with different combinations of elevation and season for each species, following Moritz et al. (2008) (Table S2, 152 species with 2,128 models in total). We constructed the occupancy models in a Bayesian framework using the package "R2jags" (Su & Yajima, 2012). We used three chains for each model and sampled 10,000 iterations (with a burn-in of the first 2000 iterations) with a thinning rate of eight samples. We chose the model with the lowest WAIC value as the best model for each species (Hooten & Hobbs, 2015). For each species, we also calculated the probability of false absence (P_{fa}) as in Tingley and Beissinger (2009) in each season using the detection probability estimated from the best model. We considered P_{fa} < 0.05 as a true absence if we did not detect the species in given elevational bands, which suggested that absence in that elevational band was not due to imperfect detection (Tingley & Beissinger, 2009). These analyses yielded 97 species for which we could determine species elevational ranges and compare seasonal changes without complications created by small sample sizes (see Liang et al., 2021).

We determined the upper-elevation limit, the lower-elevation limit, and the elevational range size of these 97 species using these criteria for true absences in elevational bands in each season. We then calculated the abundance-weighted mean elevation of these species (Ocampo-Peñuela & Pimm, 2015). The seasonal shifts in the elevation range for individual species were the differences in corresponding values from non-breeding to breeding seasons. Thus, positive values of seasonal shifts in upper-elevation limit, lower-elevation limit and abundance-weighted mean elevation represent upslope movements, while negative values represent downslope movements, and zero represents no change.

Low detection probability may bias our elevational range estimation and seasonal changes; therefore, we used occupancy models to account for the potential imperfect detections in these 152 species. Occupancy models are hierarchical models that separate survey data into two processes, the occupancy process that is mechanistic and the sampling process that is subject to detection probability (Tingley & Beissinger, 2009). We used N-mixture model structures for our occupancy models (Royle, 2004) and estimated both occurrence and detection probability in each elevational band in each season with temporal replicates (different surveys). We assumed both elevation and season (i.e. elevation, elevation^2, elevation*season, season) could affect whether a species occupies an elevational band, while detection probability could change between seasons but not among elevations. Our sampling covered a large elevational range and many of our bird data showed a unimodal distribution along elevation; hence, we included quadratic terms in our model (Moritz et al., 2008). Thus, we have 14 competing models with different combinations of elevation and season for each species, following Moritz et al. (2008) (Table S2, 152 species with 2,128 models in total). We constructed the occupancy models in a Bayesian framework using the package "R2jags" (Su & Yajima, 2012). We used three chains for each model and sampled 10,000 iterations (with a burn-in of the first 2000 iterations) with a thinning rate of eight samples. We chose the model with the lowest WAIC value as the best model for each species (Hooten & Hobbs, 2015). For each species, we also calculated the probability of false absence (P_{fa}) as in Tingley and Beissinger (2009) in each season using the detection probability estimated from the best model. We considered P_{fa} < 0.05 as a true absence if we did not detect the species in given elevational bands, which suggested that absence in that elevational band was not due to imperfect detection (Tingley & Beissinger, 2009). These analyses yielded 97 species for which we could determine species elevational ranges and compare seasonal changes without complications created by small sample sizes (see Liang et al., 2021).

We determined the upper-elevation limit, the lower-elevation limit, and the elevational range size of these 97 species using these criteria for true absences in elevational bands in each season. We then calculated the abundance-weighted mean elevation of these species (Ocampo-Peñuela & Pimm, 2015). The seasonal shifts in these four measures for individual species were the differences in corresponding values from non-breeding to breeding seasons. Thus, positive values of seasonal shifts in upper-elevation limit, lower-elevation limit and abundance-weighted mean elevation represent upslope movements, while negative values represent downslope movements, and zero represents no change.

2.4 Assessing the relationships between species traits and seasonal changes of elevational ranges

We assessed how species’ traits affected seasonal elevational shifts. Species’ traits included breeding elevation, body mass, diet, flocking status and forest dependency following the hypothesized relationships (Table S3, see Liang et al., 2021). We classified the 97 species into low-elevation (700–1,600 m a.s.l.), middle-elevation (1,600–2,800 m a.s.l.) and high-elevation breeders (2,800–3,400 m a.s.l.) based on their abundance-weighted mean elevations recorded in the breeding season. We extracted body mass and dietary groups (insectivore, omnivore, plant-seed eater and frugivore/nectarivore) from the Elton traits 1.0 database (Wilman et al., 2014). We extracted flocking status (flocking species vs. non-flocking species) from Birds of the World (Billerman et al., 2020) and an empirical database of mixed-species bird flocks in southwest China (Zhou et al., 2019). We classified two categories of forest dependency (forest birds: medium and high forest dependency; and non-forest birds: low forest dependency) provided by BirdLife International Data Zone (BirdLife International, 2020).

We used the phylogenetic generalized least-squares (PGLS) models to assess the relationships between these traits and each of the measurements of the elevational distribution shifts using package "caper" (Orme, 2013). We downloaded 5,000 phylogenetic trees of 97 target species from birdtree.org (Jetz et al., 2012) and generated a maximum clade credibility (MCC) tree using the function "maxCladeCred" in the package phangorn v2.5.5 (Schliep, 2011). We constructed four separate PGLS models for these four measures of elevational shifts. In the first model, the upper-elevation limit shift was the response variable. Body mass, breeding elevation, diet, flocking status and forest dependency were predictors. We standardized (mean of 0 and SD of 1) of the upper-elevation limit shift and body mass to increase the model homoscedasticity using the function "scale" in the basic R package (R Core Team, 2019). We selected the best models ranked by the Akaike’s information criterion corrected for small sample sizes (AICc) and subsequently averaged the coefficient of the selected models with \( \Delta \text{AIC}_c < 2 \) (comparing to the best model with the lowest AICc values) using package "MuMln" (Barton, 2020; Burnham and Anderson, 2002). We constructed the other three models with the same predictors but using the lower-elevation limit shift, the abundance-weighted mean elevation shift and the range size shift as response variables, respectively.

Finally, we used a phylogenetic paired t test to determine whether seasonal shifts in each of the four elevation metrics in 11 different trait-based and taxonomic groups were significantly different from zero (i.e. upslope, unchanged and downslope) (Lindenfor et al., 2010). The trait groups were classified by their breeding elevation and diet groups, two traits that we found were associated with elevational movements (see results). We also included two other category traits, including flocking status and forest dependency. Although no significant associations were found between elevational movements and each of the two traits (see Section 3), we cannot rule out the possibilities that any of groups classified by flocking status (flocking species, no-flocking species) and forest dependency...
(forest species, non-forest species) might also show significant elevational movements. Five major taxonomic groups are ones with more than five species, included bulbuls, Old World warblers, Old World flycatchers, Old World babblers and sunbirds (Table S4; Liang et al., 2021). We obtained phylogenetic trees for each group using the methods described previously.

We performed all analyses in R 3.8 (R Core Team, 2019).

3 | RESULTS

3.1 | Seasonal changes in species richness and community composition

We recorded 314 species during the breeding season and 296 species during the non-breeding season, yielding 368 species in total. The estimated species richness of the selected replicates reached peaks in a lower-elevational band (i.e. 1,300–1,600 m a.s.l.) in the breeding season and a middle-elevational band in the non-breeding season (1,600–1,900 m a.s.l.) (Table 1; Figure 2). Sensitivity analysis identified the same two peaks in both seasons (Table S1). We recorded reductions in species richness from the breeding to the non-breeding seasons for five of nine elevational bands (Table 1, Figure 2; Table S1). This reduction was especially evident for the highest elevational band (3,100–3,400 m a.s.l.), where estimated species richness during the non-breeding season was roughly half of that during the breeding season (Table 1; Table S1). We also recorded increases in species richness from the breeding to the non-breeding season in three of nine elevational bands in middle elevations (Table 1, Figure 2; Table S1).

Temporal beta diversity indices (TBI) decreased from low-to-middle elevations and increased rapidly with increasing elevation (Figure 3a). The B-C plot of the TBI showed that seasonal changes in species compositions resulted from species losses rather than species gains from the breeding to the non-breeding seasons, especially for lower and higher elevational bands (Figure 3b). However, in the
two middle-elevational bands (1,900–2,200 m a. s. l. and 2,200–2,500 m a.s.l.), species gains dominated losses (Table 1, Figure 3b). Among all elevational bands, however, only the two highest elevational bands showed a significant change in community composition (*p* < 0.05) (Table 1).

### 3.2 | The relationships between species’ traits and seasonal elevational shifts

PGLS models suggested that breeding elevation and diet group, but not other traits (body mass, flocking status, forest dependency) (Table 2), were important in explaining the elevational shifts of 97 species from breeding to non-breeding seasons (Figure 4). Specifically, high-elevation breeders shifted their lower-elevation limits downslope more than species that bred in middle and lower elevations (Table 2). The lower-elevation downslope limits shifted more obviously in insectivores than plant-seed eaters, whereas no differences were found between insectivores and the other two diet groups (omnivores and frugivores/nectarivores) (Table 2). Moreover, high-elevation breeders also shifted their abundance-weighted mean elevations downslope more than middle- and lower-elevation breeders (Table 2). Insectivores shifted their abundance-weighted mean elevations downslope more than frugivores/nectarivores and plant-seed eaters, but there were no differences in abundance-weighted mean elevations between insectivores and omnivores (Table 2). No traits showed correlations with the seasonal shifts on higher-elevation limits and elevational range sizes (Table 2).

### 3.3 | Seasonal elevational shifts of trait and taxonomic groups

Phylogenetic paired *t* test results indicated that high-elevation breeders shifted their upper-elevation limits, abundance-weighted mean elevations and lower-elevation limits, and the middle-elevation breeders significantly shifted their abundance-weighted mean elevations to lower elevations in non-breeding seasons (Table 3; Figure S1). In contrast, low-elevation breeders did not show differences in any of the elevation limits between the two seasons (i.e. 95% CI of the shifts overlap with zero) (Table 3). Among the diet groups, insectivores showed apparent downslope shifts in lower- and upper- elevation limits and weighted mean elevation in the non-breeding season (Figure S1). Frugivores/nectarivores also showed considerable downslope shifts in lower-elevation limits (Figure S1). On the other hand, omnivores and plant-seed eaters did not show significant seasonal shifts (Table 3).

Flocking species showed significant downslope shifts in their upper- and lower-elevation limits and weighted mean elevations, whereas non-flocking species did not show significant patterns (Table 3). Both forest and non-forest species showed significant downslope shifts in abundance-weighted mean elevations from breeding to non-breeding seasons (Table 3). While forest species also showed downslope shifts...
in lower-elevation limits, non-forest species showed downslope shifts in their upper-elevation limits (Table 3). We did not record any seasonal differences in elevational range sizes between forest dependency groups (Table 3).

For the five major taxonomic groups, only flycatchers and babblers showed significant downslope shifts, while other taxa did not show significant elevational shifts from the breeding to the non-breeding seasons (Table S4, Figure S1).

### TABLE 2
The effects of species’ traits on seasonal elevational shifts of 97 species from the breeding to the non-breeding season

| Parameters                              | Estimate | SE  | Z value | Pr(>z) | N containing best models | Sum of weights |
|-----------------------------------------|----------|-----|---------|--------|--------------------------|----------------|
| **Lower-elevation limit shift**         |          |     |         |        |                          |                |
| (Intercept)                             | −0.915   | 0.329| 2.787   | 0.005  | 7                        | 1              |
| Mean Breeding Elevation (abundance-weighted) |          |     |         |        |                          |                |
| Mean Breeding Elevation (High versus Low) | 1.015    | 0.331| 3.063   | 0.002  |                          |                |
| Mean Breeding Elevation (High versus Middle) | 0.758    | 0.316| 2.398   | 0.016  |                          |                |
| Diet                                    |          |     |         |        |                          |                |
| Diet (Insectivores versus FruiNect)     | −0.355   | 0.341| 1.040   | 0.298  |                          |                |
| Diet (Insectivores versus Omnivores)    | 0.227    | 0.247| 0.918   | 0.358  |                          |                |
| Diet (Insectivores versus PlantSeed)    | 1.420    | 0.523| 2.714   | 0.006  |                          |                |
| Forest dependency (Forest versus Non versus forest) | 0.259    | 0.239| 1.083   | 0.279  | 3                        | 0.33           |
| Flocking status (Flocker versus Non-flocker) | 0.281    | 0.223| 1.259   | 0.208  | 3                        | 0.38           |
| Body mass                               | 0.168    | 0.114| 1.467   | 0.142  | 4                        | 0.54           |
| **Abundance-weighted Mean Elevation Shift** |          |     |         |        |                          |                |
| (Intercept)                             | −1.130   | 0.295| 3.827   | <0.001 | 2                        | 1              |
| Mean Breeding Elevation (abundance-weighted) |          |     |         |        |                          |                |
| Mean Breeding Elevation (High versus Low) | 1.436    | 0.317| 4.537   | <0.001 |                          |                |
| Breeding Elevation (High versus Middle) | 0.957    | 0.298| 3.213   | 0.001  |                          |                |
| Diet                                    |          |     |         |        |                          |                |
| Diet (Insectivore versus FruiNect)      | 0.685    | 0.319| 2.146   | 0.032  |                          |                |
| Diet (Insectivore versus Omnivore)      | 0.138    | 0.229| 0.602   | 0.547  |                          |                |
| Diet (Insectivore versus PlantSeed)     | 1.367    | 0.461| 2.968   | 0.003  |                          |                |
| Forest dependency (Forest versus Non-forest) | −0.210   | 0.222| 0.948   | 0.343  | 1                        | 0.34           |
| **Upper-elevation limit Shift**         |          |     |         |        |                          |                |
| (Intercept)                             | 0.060    | 0.144| 0.416   | 0.677  |                          |                |
| Forest dependency (Forest versus Non-forest) | −0.304   | 0.228| 1.334   | 0.182  | 2                        | 0.46           |
| Flocking status (Flocker versus Non-flocker) | −0.121   | 0.212| 0.571   | 0.568  | 2                        | 0.29           |
| **Range Size Shift**                    |          |     |         |        |                          |                |
| (Intercept)                             | 0.155    | 0.193| 0.803   | 0.422  |                          |                |
| Diet                                    |          |     |         |        |                          |                |
| Diet (Insectivore versus FruiNect)      | 0.487    | 0.360| 1.351   | 0.177  |                          |                |
| Diet (Insectivore versus Omnivore)      | −0.300   | 0.258| 1.164   | 0.244  |                          |                |
| Diet (Insectivore versus PlantSeed)     | −0.426   | 0.529| 0.804   | 0.421  |                          |                |
| Forest dependency (Forest versus Non-forest) | −0.438   | 0.238| 1.845   | 0.065  | 6                        | 0.78           |
| Flocking status (Flocker versus Non-flocker) | −0.289   | 0.239| 1.211   | 0.226  | 3                        | 0.33           |
| Body mass                               | −0.173   | 0.115| 1.550   | 0.121  | 4                        | 0.54           |

Notes: For each measure of the elevational shifts (the lower-elevation limit shift, the abundance-weighted mean elevation shift, the upper-elevation limit shift and the elevational range size shift), we used a phylogenetic generalized least-squares (PGLS) model, with diet, abundance-weighted mean breeding elevation, forest dependency, flocking status and body mass as predictors. We selected the best models based on Akaike information criteria scores (ΔAICc < 2 comparing to the best model which has the lowest AICc) and averaged the coefficients of these models. Four levels of diet groups included insectivore, omnivore, plant-seed eater [PlantSeed] and frugivore/nectarivore [FruiNect]. Abundance-weighted mean breeding elevation was classified into three categories including low, middle and high elevations. Low elevations (700–1,600 m a.s.l.) were dominated by anthropogenic habitats such as cropland (Figure 1). Middle elevations (1,600–2,800 m a.s.l.) were dominated by forests. High elevations (2,800–3,400 m a.s.l.) were near or above treelines.
4 | DISCUSSION

We compared species richness and community composition of different elevational bands from the breeding to the non-breeding seasons. As predicted, we detected substantial reductions in species richness during the non-breeding season at high elevations as a result of species loss, but we also documented unexpected species loss from low elevations. We also documented increases in species richness from breeding to non-breeding seasons at middle elevations, largely a result of gains of species that bred at higher elevations moving downslope, but also from upslope shifts of some lowland-breeding birds. In general, we found only partial support for the predicted effects of species’ traits on elevational movements. As predicted, high-elevation breeders significantly shifted to lower elevations, but the predicted effects of traits other than diet were not supported. Insectivores showed the most significant downslope shifts. Species that participate in mixed-species flocks and that rely on forests also shifted to lower elevations in the non-breeding season. Our study provided empirical evidence of seasonal elevational shifts of montane birds and added to a growing literature emphasizing the importance of conserving connected elevational gradients.

4.1 | Seasonal changes in richness and community composition

From the breeding to the non-breeding season, we found reductions in species richness and loss of species in the bird communities in high and low elevations, but increases in species richness and gain of species for some middle-elevation communities. The declines of species richness at higher elevations were as predicted based on the assumption that low temperatures and declines in resources such as arthropods would leave fewer opportunities for species in many guilds in winter (Hsiung et al., 2018). Interestingly, the pattern of mid-domain peaks in diversity at middle elevations that were commonly documented in Himalayan/Hengduan Mountains from the breeding season (Katuwal et al., 2016; Pan et al., 2016, 2019) also occurred during the non-breeding season, which is consistent with another study in Taiwan (Shiu & Lee, 2003). The mid-domain effect was even stronger during the non-breeding season because there was a net loss of species from the croplands in lower elevations (i.e., two lowest elevational bands), which we did not predict. The middle elevations are critical for conserving bird communities in both seasons, as there is little apparent gain of montane species moving to the lowland sections of this gradient. Furthermore, the net loss of

![Figure 4: Species-level seasonal shifts in elevational ranges along the elevation gradient in the Gaoligong Mountains in southwest China. Elevation distributions of 97 species with sufficient data showing elevational bands where species found only in the breeding season (orange) and winter (blue), and during both seasons (grey). Species in the x-axis were ordered with decreasing abundance-weighted mean elevations.](image)
TABLE 3  Seasonal shift in elevational distributions (upper-elevation limit, abundance-weighted mean elevation, lower-elevation limit and elevational range sizes) of different trait groups

| Trait groups                        | Elevation shifts | N   | Breeding -Mean | Winter -Mean | Shift -Mean | Shift -Low 95% CI | Shift -Up 95% CI | t     | df  | P     |
|-------------------------------------|------------------|-----|----------------|--------------|-------------|-------------------|------------------|-------|-----|-------|
| Mean breeding elevation (abundance-weighted) |                  |     |                |              |             |                   |                  |       |     |       |
| High-elevation breeders (2,800–3,400 m) | Upper-elevation limit | 11  | 3,400          | 3,236        | -179        | -233             | -36              | -2.45 | 8   | 0.040 |
|                                     | Mean elevation ⁰ | 11  | 3,023          | 2,659        | -365        | -561             | -169             | -3.65 | 8   | 0.006 |
|                                     | Lower-elevation limit | 11  | 2,255          | 1,927        | -327        | -560             | -95              | -2.76 | 8   | 0.025 |
|                                     | Range size      | 11  | 1,145          | 1,309        | 164         | -68              | 395              | 1.39  | 8   | 0.203 |
| Middle-elevation breeders (1,600–2,800 m) | Upper-elevation limit | 56  | 2,929          | 2,842        | -86         | -174             | 3                | -1.89 | 53  | 0.064 |
|                                     | Mean elevation ⁰ | 56  | 2090           | 1976         | -115        | -190             | -39              | -2.97 | 53  | 0.004 |
|                                     | Lower-elevation limit | 56  | 1,171          | 1,080        | -91         | -200             | 18               | -1.64 | 53  | 0.107 |
|                                     | Range size      | 56  | 1,757          | 1,762        | 5           | -135             | 146              | -0.08 | 53  | 0.941 |
| Low-elevation breeders (700–1,600 m) | Upper-elevation limit | 30  | 2,297          | 2,190        | -90         | -245             | 65               | -1.14 | 27  | 0.264 |
|                                     | Mean elevation ⁰ | 30  | 1,236          | 1,253        | 24          | -42              | 90               | 0.72  | 27  | 0.477 |
|                                     | Lower-elevation limit | 30  | 768            | 758          | -10         | -30              | 9                | -1.02 | 27  | 0.318 |
|                                     | Range size      | 30  | 1,529          | 1,432        | -80         | -241             | 81               | -0.97 | 27  | 0.34  |
| Diet Group                          |                  |     |                |              |             |                   |                  |       |     |       |
| Frugivores/Nectarivores             | Upper-elevation limit | 9   | 2,800          | 2,800        | 0           | -226             | 226              | 0     | 6   | 0.999 |
|                                     | Mean elevation ⁰ | 9   | 1927           | 1932         | 5           | -176             | 186              | 0.06  | 6   | 0.956 |
|                                     | Lower-elevation limit | 9   | 1,333          | 1,100        | -233        | -387             | -79              | 1.23  | 6   | 0.025 |
|                                     | Range size      | 9   | 1,467          | 1,700        | 233         | -24              | 491              | 1.78  | 6   | 0.126 |
| Insectivores                        | Upper-elevation limit | 63  | 2,775          | 2,682        | -105        | -197             | -12              | -2.22 | 60  | 0.03  |
|                                     | Mean elevation ⁰ | 63  | 1923           | 1797         | -129        | -201             | -58              | -3.55 | 60  | 0.001 |
|                                     | Lower-elevation limit | 63  | 1,181          | 1,054        | -124        | -212             | 36               | -2.75 | 60  | 0.008 |
|                                     | Range size      | 63  | 1,593          | 1,628        | 19          | -112             | 150              | 0.29  | 60  | 0.776 |
| Omnivores                           | Upper-elevation limit | 21  | 2,743          | 2,586        | -186        | -610             | 237              | -0.86 | 18  | 0.399 |
|                                     | Mean elevation ⁰ | 21  | 1905           | 1,790        | -2          | -416             | 411              | -0.01 | 18  | 0.991 |
|                                     | Lower-elevation limit | 21  | 1,029          | 1,000        | -28         | -165             | 108              | -0.41 | 18  | 0.687 |
|                                     | Range size      | 21  | 1714           | 1,586        | -292        | 894              | 311              | -0.95 | 18  | 0.355 |
| Plant-Seed eaters                  | Upper-elevation limit | 4   | 2,800          | 2,950        | 150         | -105             | 405              | 1.16  | 1   | 0.454 |
|                                     | Mean elevation ⁰ | 4   | 2,233          | 2,438        | 176         | 63               | 288              | 3.06  | 1   | 0.201 |
|                                     | Lower-elevation limit | 4   | 1,600          | 1,975        | 375         | 55               | 695              | 2.29  | 1   | 0.262 |
|                                     | Range size      | 4   | 1,200          | 975          | -225        | -790             | 300              | -0.8  | 1   | 0.555 |

(Continues)
| Trait groups                          | Elevation shifts | N  | Breeding -Mean | Winter -Mean | Shift—Mean | Shift—Low 95% CI | Shift—Up 95% CI | t     | df  | P     |
|--------------------------------------|------------------|----|----------------|--------------|------------|-----------------|----------------|-------|-----|-------|
| **Flocking Group**                   |                  |    |                |              |            |                 |                 |       |     |       |
| Flockers                             | Upper-elevation limit | 49 | 2,878         | 2,774        | −86        | −169           | 3               | −2.02 | 46   | 0.049 |
|                                     | Mean elevation |
|                                    | 49 | 2042         | 1935         | −111        | −178       | −43             | −3.22           | 46    | 0.002 |
|                                     | Lower-elevation limit | 49 | 1,103         | 1,032        | −98        | −199           | 3               | −1.9  | 46   | 0.063 |
|                                     | Range size       | 49 | 1666          | 1671         | 12         | −115           | 139             | 0.19  | 46   | 0.851 |
| Non-flockers                         | Upper-elevation limit | 48 | 2,643         | 2,545        | −106       | −223           | 11              | −1.78 | 45   | 0.081 |
|                                     | Mean elevation |
|                                    | 48 | 1,755        | 1,663        | −89         | −183       | 5               | −1.86           | 45    | 0.070 |
|                                     | Lower-elevation limit | 48 | 1,098         | 1,030        | −88        | −187           | 45              | −1.72 | 45   | 0.092 |
|                                     | Range size       | 48 | 1,545         | 1,515        | −19        | −173           | 136             | −0.24 | 45   | 0.813 |
| **Forest Dependency Groups**         |                  |    |                |              |            |                 |                 |       |     |       |
| Forest species                       | Upper-elevation limit | 66 | 2,860         | 2,808        | −59        | −143           | 25              | −1.38 | 63   | 0.172 |
|                                     | Mean elevation |
|                                    | 66 | 2,060        | 1,975        | −96         | −175       | −20             | −2.47           | 63    | 0.016 |
|                                     | Lower-elevation limit | 66 | 1,244         | 1,141        | −109       | −206           | −13             | −2.22 | 63   | 0.030 |
|                                     | Range size       | 66 | 1,616         | 1,667        | 50         | −77            | 177             | 0.77  | 63   | 0.443 |
| Non-forest species                   | Upper-elevation limit | 31 | 2,519         | 2,345        | −174       | −305           | −43             | −2.61 | 28   | 0.014 |
|                                     | Mean elevation |
|                                    | 31 | 1,438        | 1,333        | −105       | −178       | −32             | −2.8            | 28    | 0.009 |
|                                     | Lower-elevation limit | 31 | 864          | 806         | −58         | −140           | 24              | −1.38 | 28   | 0.178 |
|                                     | Range size       | 31 | 1,655         | 1,539        | −116       | −265           | 32              | −1.53 | 28   | 0.137 |

Notes: For each trait group, we used the phylogenetic paired t test to compare the elevational distributions between breeding and non-breeding seasons. The negative values of shifts in elevational distributions indicated downhill, while positive values of elevational distribution shifts suggested uphill. Significant differences are marked in bold (95% CI of shifts do not overlap with zero).

*The mean elevation was abundance-weighted.*
species in non-breeding seasons partially resulted from the absence of summer breeders (e.g., Blue-tailed Bee-eater *Merops philippinus* and Plaintive Cuckoo *Cacomantis merulinus*) that migrate south to Southeast Asia or Peninsular India during the non-breeding season.

### 4.2 Seasonal elevational shifts among different trait groups

As predicted, high- and middle-elevation breeders showed apparent downslope movements in the non-breeding season, even among closely related species. In *Aethopyga* sunbirds, for example, the middle- and higher-elevation breeders (*Mrs Gould's Aethopyga gouldiae*, Green-tailed *A. nipalensis*, and Fire-tailed *A.a ignicauda* sunbirds) showed substantial downslope shifts (see Liang et al., 2021). In contrast, we detected no significant upslope movement into the forest of all low-elevation species, although some of the low-elevation breeders (e.g. the Black-throated Sunbird *A. saturata*) did show some upslope movements (see Liang et al., 2021), which is consistent with a recent study in Taiwan (Tsai et al., 2021). Insectivores also shifted their abundance-weighted mean elevations downslope in the non-breeding season. Harsh climatic conditions and reduced food availability in winter are likely to drive the downslope movements of species directly or indirectly (Boyle, 2011; Boyle et al., 2010; Hsiung et al., 2018). In our study region, low temperature and partial snow cover in winter may reflect differing physiological tolerances (DuBay et al., 2020) and decrease the foraging opportunities of species that breed in higher elevations. Compared with omnivores and other diet groups, the movements of insectivores such as babblers and flycatchers were more pronounced than those that depend on less seasonal fruits and seeds. In montane areas, arthropod abundances generally decrease from the breeding to the non-breeding seasons, and this decrease may be particularly evident at high elevations (Ghosh et al., 2011; Ghosh-Harih & Price, 2014; Xue, 1995).

Species that rely on forests and participate in mixed-species flocks also showed significant downslope shifts from the breeding to the non-breeding seasons. Such downslope movements may be particularly challenging for those groups in montane areas in southwest China where low-to-middle elevations have experienced the greatest rates of deforestation and are less protected (Pan et al., 2019). Our results differ considerably from those of Elsen et al. (2017), who documented shifts of many forest species into human-dominated, non-forest habitats in winter. In these northern Himalayan ecosystems, agricultural land conversion tends to be less extreme than it is in our study region, where the lowlands have been almost entirely converted to intensively managed row crops and coffee (Pan et al., 2019; Xue, 1995). The less-intensive land use of the northern Himalayas studied by Elsen et al. (2017) may be easier for forest species to exploit in winter. Temperate forests of the northern Himalayas may also offer fewer insect resources in the non-breeding season than the subtropical forests in Yunnan, where insectivores remained in forests rather than switch to more disturbed, agricultural habitats in the lowlands. Indeed, about half of lowland species (16 out of 30) moved upslope in the non-breeding season, possibly shifting to more forested habitats (See Liang et al., 2021).

Recent studies showed that human disturbance modifies complex species interactions of mixed-species flocks in different habitats in montane areas (Mammides et al., 2015). In our research areas, for instance, *Alicpe* fulvetta-led mixed-species flocks and forest specialists were less frequent in degraded natural forests and agricultural areas, which are mainly in low-to-middle elevations, than in middle-to-high-elevational forests in the non-breeding season (Zhou et al., 2019). Nevertheless, it is unclear whether the downslope elevational shifts of forest species and flocking species in our research site will cause some fitness-related costs. Thus, further studies of population-based survival estimates and individual-based tracking may help to understand the consequences of the downslope shifts of these groups in the non-breeding season (Guillaumet et al., 2017; Srinivasan, 2019).

Species' body mass was not associated with seasonal shifts in elevation, which contrasts with a recent study in Taiwan (Tsai et al., 2021), where smaller-bodied species shifted their distribution centre to lower elevations more than large-bodied species in the non-breeding season. The sites at different elevations in our gradient were also close together geographically than those in Taiwan, which may mean that larger-bodied birds would have less trouble moving among sites at different elevations. Our sample sizes for some rare species of high conservation priority, however, were too small for our analyses, which means that we may have missed some elevational movements of larger, less abundant species. We may also have missed some important elevational shifts of rare species of conservation concern that have very restricted elevational ranges. The Fire-tailed Myzornis *Myzornis pyrrhula*, for example, which bred at and above tree line may have very narrow winter ranges in far lower elevations, but our data did not meet our sample size requirements. Further studies with more intensive sampling should therefore focus on these species, which may be more restricted in their habitat requirements than commoner, more widespread species.

### 4.3 Conclusions and conservation implications

Our study reinforces the results of other studies (Maicher et al., 2020) in suggesting that seasonal range shifts should not be ignored when designing conservation strategies to preserve biodiversity in montane ecosystems. Montane areas in Asia are experiencing substantial rates of deforestation, beginning with lower elevations and gradually moving upslope to higher elevations (Edwards et al., 2019; Feng et al., 2021; Sodhi et al., 2004). Unlike the situation further north in the Himalayas (Elsen et al., 2017), we found evidence that only a few forest species shift in winter to these anthropogenic habitats (Figure 4, Liang et al., 2021). Therefore, conserving forests in the middle elevations (i.e., 1,300–1,900 m) may be especially critical as they have high diversity at all seasons and are especially heavily used during the winter. Yet, most of the nature reserves in southwest
China cover few that range from low-to-middle elevations where bird diversity in the breeding season and winter is richest (Wang et al., 2000; Wu et al., 2010). In our research areas, for instance, the majority (87.5%) of protected areas (i.e. nature reserves) are located above 2,000 m (Lan & Dunbar, 2000; Xue, 1995). Thus, the ongoing and future land-use change at low and middle elevations are likely to erode the connectivity of forests on which elevational migrants rely (Feng et al., 2021; Powell & Bjork, 2004). Together, we recommend that additional conservation efforts should be focused on expanding nature reserves to increase habitat connectivity across the elevational gradients, especially by increasing preservation and restoration of forests in low and middle elevations. In addition, research efforts to understand how animal communities respond to agricultural practices such as coffee plantations might provide valuable insights into making agricultural landscapes more useful for birds. Although we only focused on a single mountain, implications and conservation recommendations of our results could apply to other mountains in Asia, particular southwest China, where protected areas covered only a small proportion of lands in low elevations (Wu et al., 2010, 2013, 2017).

ACKNOWLEDGEMENTS
We are grateful to Ge Gao, Wei Zeng, Wande Li, Xuejing Wang, Danjie Li, Yingying Feng, Guansheng Wang, Xi Chen, Binqiang Li, Haotian Bai, Linzhuang Bai, Teng Tang, Xin Lin, Chen Zeng, Xuelian Zhang and Wenyi Zhou, for their help in the field, and Jianchao Liang for help with preparing the map. We thank Fengyi Guo and Fangyuan Hua for their comments on the early version of the manuscript. This work was supported by grants from the National Natural Science Foundation of China (grant numbers 31700350) to XP, the Ma Huateng Foundation to DL, the Fundamental Research Funds for the Central Universities (Grant numbers 161py34) to YL and the National Natural Science Foundation of China (Grant numbers 32060118) to XL.

CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://publo ns.com/publon/10.1111/ddi.13420.

DATA AVAILABILITY STATEMENT
The dataset that support the findings of this study is available at https://doi.org/10.5061/dryad.rxwdbrv6c (Liang et al., 2021).

REFERENCES
Barçante, L., Vale, M. M., & Alves, M. A. S. (2017). Altitudinal migration by birds: A review of the literature and a comprehensive list of species. Journal of Field Ornithology, 88(4), 321–335. https://doi.org/10.1111/jfo.12234
Bibby, C. J., Burgess, N. D., Hill, D. A., & Mustoe, S. (2000). Bird Census Techniques. Elsevier.
Billerman, S. M., Keeney, B. K., Rodewald, P. G., & Schulenberg, T. S. (2020). Birds of the World. Cornell Laboratory of Ornithology. https://birds.oftheworld.org/bow/home
BirdLife International (2020). IUCN Red List for birds. Downloaded from http://www.birdlife.org. 20/05/2020
Boyle, W. A. (2011). Short-distance partial migration of Neotropical birds: A community-level test of the foraging limitation hypothesis. Oikos, 120(12), 1803–1816. https://doi.org/10.1111/j.1600-0706.2011.19432.x
Boyle, W. A., & Martin, K. (2015). The conservation value of high elevation habitats to North American migrant birds. Biological Conservation, 192, 461–476. https://doi.org/10.1016/j.biocon.2015.10.008
Boyle, W. A., Norris, D. R., & Guglielmo, C. G. (2010). Storms drive altitudinal migration in a tropical bird. Proceedings of the Royal Society B: Biological Sciences, 277(1693), 2511–2519. https://doi.org/10.1098/rspb.2010.0344
Dehling, D. M., Fritz, S. A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K., & Schleuning, M. (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography, 37(11), 1047–1055. https://doi.org/10.1111/ecog.00623
Dray, S., Bauman, D., Blanchet, G., Borcard, D., Claype, S., Guenard, G., & Wagner, H. H. (2020). adespatial: Multivariate Multiscale Spatial Analysis (Version 0.3-8). https://CRAN.R-project.org/packag es/adespatial
DuBay, S. G., Wu, Y., Scott, G. R., Qu, Y., Liu, Q., Smith, J. H., Xin, C., Hart Reeve, A., Juncheng, C., Meyer, D., Wang, J., Johnson, J., Cheviron, Z. A., Lei, F., & Bates, J. (2020). Life history predicts flight muscle phenotype and function in birds. Journal of Animal Ecology, 89(5), 1262–1276. https://doi.org/10.1111/1365-2656.13190
Dumbacher, J. P., Miller, J., Flannery, M. E., & Xiaojun, Y. (2011). Avifauna of the Gaoligong Shan Mountains of western China: A hotspot of avian species diversity. Ornithological Monographs, 70, 30–63. https://doi.org/10.1525/om.2011.70.1.30
Edwards, D. P., Socolar, J. B., Mills, S. C., Burivalova, Z., Koh, L. P., & Wilcove, D. S. (2019). Conservation of tropical forests in the Anthropocene. Current Biology, 29(19), R1008–R1020. https://doi.org/10.1016/j.cub.2019.08.026
Elsen, P. R., Kalyanaraman, R., Ramesh, K., & Wilcove, D. S. (2017). The importance of agricultural lands for Himalayan birds in winter: Himalayan Birds on Agriculture Land. Conservation Biology, 31(2), 416–426. https://doi.org/10.1111/cobi.12812
Elsen, P. R., Monahan, W. B., & Merenlender, A. M. (2018). Global patterns of protection of elevational gradients in mountain ranges. Proceedings of the National Academy of Sciences, 115(23), 6004–6009. https://doi.org/10.1073/pnas.1720141115
Elsen, P. R., Ramesh, K., & Wilcove, D. S. (2018). Conserving Himalayan birds in highly seasonal forested and agricultural landscapes: Conserving Himalayan Birds. Conservation Biology, 32(6), 1313–1324. https://doi.org/10.1111/cobi.13145
Feng, Y., Ziegler, A. D., Elsen, P. R., Liu, Y., He, X., Spracklen, D. V., Holden, J., Jiang, X., Zheng, C., & Zeng, Z. (2021). Upward expansion and acceleration of forest clearance in the mountains of Southeast Asia. Nature Sustainability, https://doi.org/10.1038/s41893-021-00738-y
García-Navas, V., Sattler, T., Schmid, H., & Özgül, A. (2020). Temporal homogenization of functional and beta diversity in bird communities of the Swiss Alps. Diversity and Distributions, 26(8), 900–911. https://doi.org/10.1111/ddi.13076
Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng, P. K. L. (2004). Southeast Asian biodiversity: An impending disaster. *Trends in Ecology & Evolution*, 19(12), 654–660. https://doi.org/10.1016/j.tree.2004.09.006

Srinivasan, U. (2019). Morphological and behavioral correlates of long-term bird survival in selectively logged forest. *Frontiers in Ecology and Evolution*, 7. https://doi.org/10.3389/fevo.2019.00017

Su, Y.-S., & Yajima, M. (2012). *R2jags: A Package for Running jags from R*. R package version 0.03-08. https://CRAN.R-project.org/package=R2jags

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

Tingley, M. W., & Beissinger, S. R. (2009). Detecting range shifts from historical species occurrences: New perspectives on old data. *Trends in Ecology & Evolution*, 24(11), 625–633. https://doi.org/10.1016/j.tree.2009.05.009

Tsai, P.-Y., Ko, C.-J., Chia, S. Y., Lu, Y.-J., & Tuanmu, M.-N. (2021). New insights into the patterns and drivers of avian altitudinal migration from a growing crowdsourcing data source. *Ecography*, 44(1), 75–86. https://doi.org/10.1111/ecog.05196

Wang, Z., Carpenter, C., & Young, S. S. (2000). Bird distribution and conservation in the Ailao Mountains, Yunnan, China. *Biological Conservation*, 92(1), 45–57. https://doi.org/10.1016/S0006-3207(99)00058-0

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). *EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals*. Ecology, 95(7), 2027. https://doi.org/10.1890/13-1917.1

Wu, F., Yang, X. J., & Yang, J. X. (2010). Additive diversity partitioning as a guide to regional montane reserve design in Asia: An example from Yunnan Province, China. *Diversity and Distributions*, 16(6), 1022–1033. https://doi.org/10.1111/j.1472-464x.2010.00710.x

Wu, Y., Colwell, R. K., Rahbek, C., Zhang, C., Quan, Q., Wang, C., & Lei, F. (2013). Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *Journal of Biogeography*, 40(12), 2310–2323. https://doi.org/10.1111/jbi.12177

Wu, Y., DuBay, S. G., Colwell, R. K., Ran, J., & Lei, F. (2017). Mobile hotspots and refugia of avian diversity in the mountains of southwest China under past and contemporary global climate change. *Journal of Biogeography*, 44(3), 615–626. https://doi.org/10.1111/jbi.12862

**BIOSKETCH**

Dan Liang is a conservation scientist who is interested in understanding how anthropogenic disturbance affects populations, species and ecosystem services.

Xinyuan Pan is a community ecologist who is interested in understanding the spatial and temporal patterns of montane biodiversity.

All authors share interests in biodiversity and conservation of montane birds.

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

**How to cite this article:** Liang, D., Pan, X., Luo, X., Wenda, C., Zhao, Y., Hu, Y., Robinson, S. K., & Liu, Y. (2021). Seasonal variation in community composition and distributional ranges of birds along a subtropical elevation gradient in China. *Diversity and Distributions*, 27, 2527–2541. https://doi.org/10.1111/ddi.13420