Seasonal elevational patterns and the underlying mechanisms of avian diversity and community structure on the eastern slope of Mt. Gongga

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Abstract
Aim: Mountain ecosystems harbour significant biodiversity across elevations and seasons. This biodiversity, however, is increasingly under threat from climate change and human land use. While much work has been done to characterize biodiversity in tropical mountains, far less is known about the environmental, seasonal and spatial factors that impact diversity and community structure in subtropical and temperate regions.

Location: Mt. Gongga, Sichuan, China: the eastern-most peak in Asia above 7000-m elevation and the main peak of the Hengduan Mountains.

Method: We examined elevational patterns and ecological variables underlying taxonomic diversity (TD), phylogenetic diversity (PD), functional diversity (FD) and community structure in birds on the eastern slope of Mt. Gongga between 1100- and 4400-m elevation. We assessed biodiversity patterns between species with different elevational range sizes (small- vs. large-ranged species) and between seasons (breeding vs. non-breeding season).

Results: We recorded 230 bird species across seven field surveys. TD, PD and FD showed similar hump-shaped elevational patterns in both seasons. In the breeding season, TD, PD and FD for small-ranged species were highly correlated with climatic factors (mean daily temperature, seasonal temperature range) and vegetation factors (enhanced vegetation index), while large-ranged species were correlated with spatial factors (mid-domain effect). In the non-breeding season, TD, PD and FD for all species groupings were positively correlated with climate factors. For small-ranged species in both seasons, community structure was more overdispersed at low and high elevations, and more clustered at middle elevations. For large-ranged species, community structure differed between seasons, showing a general trend towards clustering as elevations increase in the breeding season and trends towards overdispersion and/or evenness as elevations increase in the non-breeding season.

Conclusions: We found that different factors shape elevational patterns of diversity for small- and large-ranged species in the breeding season; small-ranged species are...
shaped by climate and vegetation structure, while large-ranged species are shaped by spatial factors. This difference is likely explained by differences in ecological niche breadth (physiological tolerance and/or habitat specialization) between small-ranged species and large-ranged species. In the non-breeding season, however, when climate is seasonally harsher, we found that patterns of diversity for all range-size groupings were driven by climatic factors. We also found that community structure generally becomes more overdispersed as resource availability decreases and environmental conditions become harsher, like at higher elevations and in the non-breeding season, suggesting that competition for limited resources is important for shaping communities in seasonal environments. These findings highlight how avian diversity and community structure are dynamic across a local elevational gradient and seasonally, shifting across the annual cycle, which has implications for conservation strategies and land management.

KEYWORDS
bird diversity, breeding season, community structure, competition, elevational gradient, Gongga Mountain, habitat filtering

1 INTRODUCTION

Studying patterns of biodiversity across space and time can help us understand the mechanisms that shape community composition (Sutherland et al., 2013). The number of species in a community, known as taxonomic diversity (TD), is commonly used to characterize biodiversity and species assemblages (He et al., 2019; Pan et al., 2016; Pavoine, & Bonsall, 2011), but taxonomic diversity alone ignores other axes of variation that exist within a community, such as variation in ecology (functional diversity) and the degree of relatedness among species (phylogenetic diversity) (Tscharntke et al., 2012). Functional diversity (FD), which can be calculated from species’ trait data, reflects the scope of functional traits within an assemblage, providing insight into the ecological uniqueness, redundancy or complementarity within a community. Compared to TD, FD might better reflect the degree of maintenance, resistance or resilience of ecosystems in the face of species loss (Petchey, & Gaston, 2002; Burgio et al., 2019). In addition, phylogenetic diversity (PD) reflects the phylogenetic variation among species and the evolutionary history of a community (Faith, 1992; Hanz et al., 2019). Comparisons of TD, FD and PD can offer complementary information and together can help us better understand the ecological and environmental mechanisms that shape patterns of biodiversity and community structure (Hanz et al., 2019; McGill et al., 2006).

Functional and phylogenetic data are often used to assess deterministic processes of community assembly (He et al., 2018; Liao et al., 2020; Webb et al., 2002; Xu et al., 2017), such as environmental filtering and interspecific competition, which can result in non-random community structure (Liao et al., 2020; Montano-Centellas et al., 2019). Environmental filtering, in which fitness of a species is impacted by environmental conditions (like temperature or water availability), results in phylogenetically and/or functionally clustered biological communities (i.e. species that are more closely related, with more similar functional traits), while interspecific competition can reduce ecological and phylogenetic similarity among species, resulting in phylogenetic and/or functional overdispersion (i.e. species that are more distantly related, with less similar function traits) (Gomez et al., 2010; Sobral, & Cianciaruso, 2016). By comparing functional and phylogenetic diversity, we can begin to tease apart the various processes that shape community composition. For example, if functional traits are phylogenetically conserved, phylogenetic clustering of a community (more similar than expectation) may be the product of environmental filtering, while an overdispersed phylogenetic structure would suggest that interspecific competition plays a role in define community composition. However, if functional traits are phylogenetically convergent, environmental filtering could result in community overdispersion, while interspecies competition would then produce a random or clustered community structure (Webb et al., 2002).

In this study, we compare elevational patterns of diversity (TD, PD and FD) and community structure in birds on the eastern slope of Mt. Gongga in Sichuan, China, on the eastern edge of the Tibetan Plateau. We compare diversity metrics between species with different contemporary elevational range sizes (small- vs. large-ranged species), as well as between seasons (breeding vs. non-breeding season). We also test the role of geographic factors (like land area and mid-domain effect; Colwell et al., 2004; Elsen & Tingley, 2015) and environmental factors (like temperature, precipitation, vegetation and invertebrate biomass; Hurlbert, & Haskell, 2003; Koh et al., 2006; Price et al., 2014; Wu, Colwell, et al., 2013) in explaining elevational patterns of diversity at a local scale. Two key features of this research include the following: (1) we assessed diversity patterns for species with different elevational range sizes, which may have experienced different historical pressures and constraints given their contemporary distributions, and (2) we assessed seasonal changes in biodiversity, as seasonality plays an important role in defining
life history, ecology and distribution (Hurlbert, & Haskell, 2003). By jointly analysing various metrics of diversity, and their changes along a steep environmental gradient and over the course of the year, we hope to better understand how biotic and abiotic factors interact to shape avian communities in the seasonally dynamic and biologically rich temperate mountains of Asia.

2 | METHODS

Mt. Gongga is located in the transition zone between the Sichuan Basin and the Qinghai–Tibetan Plateau (29°20′-30°39′N, 101°30′-102°12′E, Figure 1). It is the highest peak in the Hengduan Mountains, with an elevational range of approximately 6400 m from the bank of Dadu River (1100 m) to the summit (7556 m). The planimetric distance along the eastern slope of Mt. Gongga from the foot of the mountain to the summit is only 29 km (Zhong, 1999). The mountain has a complex geological structure, varied geomorphologic types, and high species richness and regional endemism (Wu et al., 2017; Zhong, 1999). The eastern slope of Mt Gongga exhibits striking elevational zonation in vegetation along the steep elevational gradient (from low to high elevation: sparsely wooded shrub and grass sub-belt, agroforestry belt, evergreen broadleaf forest sub-belt, evergreen broadleaf forest and deciduous broadleaf mixed forest belt, coniferous and deciduous broadleaf mixed forest belt, montane dense coniferous forest belt, shrub and grass belt, and remnant meadow and rock-scrub belt) and climatic zonation (Dry-Warm valley climate, subtropical climate and alpine climate) (Cheng, & Luo, 2002; Zhong, 1999).

2.1 | Bird survey

We conducted seven field surveys of birds from 1100 to 4400 m asl. between 2012 and 2018, four in the breeding season between April and August (two in 2012, one in 2017, one in 2018) and three in the non-breeding season between November and March (two in late autumn/early winter, from November to December in 2017 and in 2018, and one primarily in March 2016). The March survey in 2016 was limited to elevations between 1100 and 3200 m asl. because of heavy snow pack above 3000 m asl. The lower elevational limit of the transect was set by the Dadu River, and the upper elevational limit was set by the presence of heavy snow pack. We divided the elevational gradient into eight elevational sampling bands of 400 m each, and bird surveys spanned entire elevational bands.

Within each sampling band, transects were 1.5-3 km in length and were set to span main vegetation types. Survey methods were modified and improved slightly in the different survey years due to weather and inaccessibility, largely because of landslides and/or dense vegetation growth. Modifications included survey intensity, surveyors and time of day. For example, in 2012 and 2016, surveys were conducted from dawn to dusk, while in 2017 and 2018, surveys were conducted during dawn and dusk (4 h after sunrise and 4 h before sunset), skipping the less active middle part of the day. Some transects (1600–2000 m, 2000–2400 m, 4000–4400 m) were moved in 2017 and 2018 to areas near original transect locations because of increasing human disturbance and/or landslides. These modifications, however, should not affect our overall conclusions about species richness patterns because the overall survey intensity was kept the same in each elevation band during the whole survey period, and because we present results as an aggregate of the years for each elevational band.

For each survey, we recorded the presence and abundance of bird species using a line transect method. While surveying, we identified all birds by sight and sound, recording the time and elevation (to the nearest 50 m interval). Two line transect surveys were conducted in each elevational band in 2012 and 2016, except at the highest elevational band (only one line transect survey was conducted), from dawn to dusk by walking slowly to record

![Figure 1](image-url) Location of study, invertebrate sampling sites and bird survey transects. The study area was separated into 8 sampling elevational bands (from 1100 to 4400 m), Bird survey transects are indicated by pink lines for 2012 and 2016, while by dark lines for 2017 and 2018.
all individual birds seen or heard. Most surveys were carried out along available trails and roads. In 2017 and 2018, to increase the probability of detecting elusive or rare species, for all transects, surveys were carried out twice each morning and twice each evening (one survey walking upslope and one survey walking downslope, separated by 20 min), for a total of four surveys per transect in each survey band (following methods in Elsen et al., 2017). The locations of the eight 400-m elevational transects can be seen in Figure 1.

2.2 | Spatial and environmental factors

To test how land area influences species diversity, we calculated land area for each 400-m band within the valley using ArcGIS 10.2 (ESRI, Redlands, CA, USA) and based on STRM 90-m digital elevation data from CGIAR-CSI (http://srtm.cgiar.org/) (Figure 1).

For each season (the breeding season: April to August, the non-breeding season: November to March), we calculated mid-domain effect (MDE) using bird distribution data. We also calculated enhanced vegetation index (EVI), mean daily temperature (MDT), seasonal precipitation (SP; the total precipitation), seasonal temperature range (STR; the difference between the mean temperature of the coldest and warmest months in the season) and mean temperature of the coldest month (MTC) using environmental data. The specific methods for each metric are detailed below.

Mid-domain effect (MDE): We used RangeModel 5 (http://viceroy.eeb.uconn.edu/estimates/) to calculate interpolated species richness and estimate predicted species richness under "pure" geometric constraints (assuming no interaction with other factors; Colwell, 2008). We ran 5000 randomizations of the MDE null model (random range placement) to get mean expected species richness with 95% confidence interval for each elevational band.

Enhanced vegetation index (EVI): As a proxy for above-ground net primary productivity, we averaged EVI data from 2014 and 2015 for each elevational band. EVI was calculated using ArcGIS 10.2 (ESRI, Redlands, CA, USA). All remote sensing data were downloaded from Geospatial Data Cloud (http://www.gcloud.cn/sources/).

Daily mean temperature (MDT), seasonal precipitation (SP), seasonal temperature range (STR) and mean temperature of coldest month (MTC): we calculated these metrics in each 400-m elevational band based on daily records from the five local meteorological stations and three temperature/relative humidity smart sensors (SSN-22E, Yowexa, Shenzhen, China) in Hailugou Valley in 2016. The five meteorological stations were established by the Institute of Mountain Hazards and Environment and located at 1600 m, 2300 m, 2800 m, 3000 m and 3350 m, and the three smart sensors were placed at 1200 m, 2000 m and 4000 m. We used linear (for MDT) and LOESS (for SP, MTC and STR) regressions to estimate climatic variables for each elevational band along the elevational gradient. Sites without climate records were linearly or curvilinearly extrapolated or interpolated based on the data from nearby sites.

2.3 | Diversity metrics of bird assemblages

We assessed how elevational range size of birds is associated with elevational patterns of species diversity (taxonomic diversity, phylogenetic diversity and functional diversity) and community structure by grouping birds into one of two elevational range size categories based on a species’ annual elevational distribution at the study site: "large-ranged species," with elevational ranges equal to or above the median elevational range (1600 m) for species in the dataset; and "small-ranged species," with elevational ranges below 1600 m (Pandy et al., 2020; Wu, Yang, et al., 2013).

2.3.1 | Taxonomic diversity

A total of 230 bird species were recorded from the eastern slope of Mt. Gongga across the seven surveys. Of these species, 17 species were removed from the dataset for subsequent analyses to reduce error in interpretations. These species include the following: four waterfowl species (because they are distributed along watercourses and their distributions may not be driven by elevation itself), seven raptors species, three swift species and three swallow species (because they were predominately detected in flight above the observer and their elevational distribution were difficult to define). Consequently, 213 bird species were used in the subsequent analyses, with a total of 200 species in the breeding season and 117 species in the non-breeding season. Based on their elevational range sizes, we classified 72 species as large ranged and 128 species as small ranged in the breeding season, and 51 species as large ranged and 66 species as small ranged in the non-breeding season (Figure 2, Appendix S3).

The number of bird species recorded in each elevational band was used as the observed species richness. Because of the difficulty detecting all species in natural communities through short-term surveys, we used non-parametric estimators (Chao2, ACE, Jackknife 1 and Jackknife 2) and interpolation to estimate species richness (Burnham & Overton, 1979; Chao & Chiu, 2012; Colwell & Coddington, 1994; Colwell et al., 2004; McCain, 2004). All non-parametric estimators were calculated by the function "ChaoSpecies" in the R package “SpadeR” (Chao et al., 2016). We then interpolated species richness (species were assumed to occur at an elevation if they were detected at both higher and lower elevation) to reduce survey error. This approach is often considered appropriate for vagile species along local gradients where suitable habitat is continuous, because gaps in recorded distribution are more likely attributable to incomplete sampling rather than to true gaps of species distribution on a local scale, especially when gaps are found only for rare species (Wu, Yang, et al., 2013). We found that the patterns of estimated species richness were similar to and highly correlated with interpolated species richness, which we used for subsequent analyses (Figure S1).

We defined the elevational range limits for each species at a resolution of 50 m, based on the highest and lowest points of detection across surveys for each season.
2.3.2 | Phylogenetic diversity

To analyse PD, we extracted phylogenies of the recorded species from a published super-tree of birds (Jetz et al., 2012, 2014). We downloaded 10,000 trees from BirdTree (http://birdtree.org) under the option of “Hackett All Species: a set of 10,000 trees with 9993 OTUs each.” Subsequently, we sampled 5000 pseudo-posterior distributions and constructed the Maximum Clade Credibility tree using mean node heights with TreeAnnonator v1.10.4 in the BEAST package (Si et al., 2017; Suchard et al., 2018). The resulting species trees for birds in Hailuogou Valley are shown in Figures S2 and S3 (200 species and 117 species as the species pools for breeding and non-breeding seasons, respectively). PD was then calculated as the averaged Faith’s index, which is the sum of branch lengths of the phylogenetic tree for all species within a given community (Faith, 1992). We used the “PhyloMeasures” package in R to calculate phylogenetic diversity (Tsirogiannis, & Sandel, 2016).

2.3.3 | Functional diversity

To calculate FD, we collected data on 23 traits that are associated with body features, as well as feeding and breeding ecology in birds (Liao et al., 2020; Zhang et al., 2020). We compiled trait data from The Handbook of the Birds of China for each species found in our surveys (Zhao, 2001). The 23 traits include the following: seven continuous traits (body mass, body length, tail length, tarsometatarsus length, culmen length, wing length, clutch size) and 16 categorical traits (4 binary diet traits, 6 binary feeding stratum traits and 6 binary nesting habitat traits). Diet, main feeding stratum and nesting habitats were binomial (scored as either 0 or 1) and are commonly used in the studies of bird functional diversity as they relate to resource requirements and sensitivity to habitat change (Petchey et al., 2007; Si et al., 2016). All traits are presented in Appendix S2. We calculated FD as the sum of branch lengths of the functional dendrogram for all species in a community (Petchey, & Gaston, 2002). To calculate the function distance matrix (Gower distance), we used the function “vegdist” in the R package “vegan” (Oksanen et al., 2013). We clustered the function distance matrix to get the functional dendrogram (Figures S4 and S5). We then calculated FD based on the functional dendrogram, following methods similar to PD.

2.3.4 | Phylogenetic signal

We quantified the phylogenetic signal for life history and morphological trait data to identify differences between PD and FD. If a significant phylogenetic signal was detected in a trait, it
suggests that closely related species have higher trait similarity than expected by chance (Revell et al., 2008). For continuous traits, we quantified the phylogenetic signal using the K statistic. A value of $K \geq 1$ suggests a significant phylogenetic signal in trait data that departs from a model of trait evolution under Brownian motion (i.e. trait conservatism), while a value of $K < 1$ suggests less trait conservatism than expected under a model of Brownian motion (i.e. trait convergence) (Blomberg et al., 2003). For binary traits, we quantified the phylogenetic signal using the D statistic. If $D$ approaches 0, then there is conserved trait evolution. $D < 0$ suggests trait clustering. A value of $D \geq 1$ indicates no phylogenetic signal or that a trait is overdispersed on the phylogenetic tree (Fritz, & Purvis, 2010). The D and K statistics were calculated using “phylo.d” and “multiPhylosignal” functions in the “caper” and “picante” packages, respectively (Kembel et al., 2010; Orme et al., 2013).

2.4 | Phylogenetic and functional structure

We used the function “ses.mpd” and the null model “taxa.labels” in the R package “picante” to compute the standardized effect size of mean phylogenetic distances (SES.MPD), which assesses phylogenetic relatedness in community assemblages (Webb et al., 2002). A positive value of SES.MPD indicates that species in a community are more distantly related than expected (overdispersed), which is consistent with interspecific competition, while a negative value of SES.MPD indicates that species are more closed related than expected (clustered), which is consistent with environmental filtering (Webb et al., 2002). SES.MPD is computed as

$$\text{SES.MPD} = \frac{\text{MPD}_{\text{obs}} - \text{meanMPD}_{\text{null}}}{\text{sdMPD}_{\text{null}}}$$

where $\text{MPD}_{\text{obs}}$ is the observed mean phylogenetic distance (MPD) of birds in a community, $\text{meanMPD}_{\text{null}}$ is the mean MPD of the null models (shuffle distance matrix labels 999 times), and $\text{sdMPD}_{\text{null}}$ is the standard deviation of MPD of the null models.

We also calculated standardized effect size of mean functional distances (SES.MFD) based on the functional dendrogram, following methods similar to the standardized effect size of mean phylogenetic distances (SES.MPD). A positive value of SES.MFD suggests that species in a community are more functionally disperses than expected by chance, consistent with interspecific competition, while a negative value of SES.MFD suggests that environmental filtering may result in more functional clustering within the community (Webb et al., 2002).

2.5 | Statistical analysis

We used Spearman correlation to examine the relationships among the independent variables (land area, MDT, SP, STR, EVI, MDE and MTC, Table S1 and S2), as well as the relationship between species diversity and community structure within the same range size groupings. We performed simple ordinary least squares (OLS) regression to examine the potential of individual variables to explain elevational patterns of TD, PD, FD, SES.MPD and SES.MFD for each species groupings (all species together, and large- and small-ranged species separately). All analyses were performed in R 4.0.5 (https://www.r-project.org/).

3 | RESULTS

3.1 | Elevational patterns of environmental variables, biodiversity and community structure

The environmental variables show different elevational patterns. Land area had two distinct peaks along the elevation gradient: land area peaked at 1800 m and 3000 m (Figure 3). During the breeding season, SP and STR peaked at 3400 m and 3800 m, respectively, and EVI peaked at 1800 m. MDT and MTC generally decreased as elevation increased. During the non-breeding season, EVI peaked at 1400 m and 1800 m, while MDT, STR and MTC generally decreased and SP generally increased as elevation increased (Figure 3).

TD, PD and FD were positively correlated with each other for all range-size groupings in both seasons. As expected, elevational patterns of diversity differed between seasons (Figure 4). In the breeding season, the diversity--elevation relationships for total, small- and large-ranged species all showed hump-shaped patterns. The diversity--elevation curves for total and small-ranged species peaked at 2200 m, and large-ranged species peaked at 3000 m. In the non-breeding season, the diversity--elevation relationships for total, small- and large-ranged species also showed hump-shaped patterns, with peaks shifting to lower elevation (1800 m; Figure 4).

When we compared analyses that use the seasonal species pools with analyses that use the total species pool, we found largely congruent patterns between the two methods (Figure S6). We thus report results using seasonal species pools in the main text. SES.MPD and SES.MFD were significantly positively correlated for total and small-ranged species in both seasons, and SES.MPD and SES.MFD were weakly correlated for large-ranged species in both seasons (Tables S3 and S4). In the breeding season, total and small-ranged species were phylogenetically and functionally clustered at middle elevations (SES.MPD and SES.MFD $< 0$) and were more phylogenetically and functionally dispersed at low and high elevations than at middle elevations (Figure 4). Large-ranged species were more phylogenetically and functionally clustered at high elevations than at low elevations (Figure 4). In the non-breeding season, phylogenetic and functional structure of small-ranged species showed irregular elevational patterns. Phylogenetic structure of total and large-ranged species were clustered at low elevations and show a more dispersed trend towards higher elevations, while functional structure of large-ranged species was more dispersed at middle elevations than at low and high elevations. In addition, SES.MPD and SES.MFD for
all species groupings were not calculated for the highest elevation band (4000–4399 m) where we observed zero or only one bird species in a survey.

### 3.2 Phylogenetic signals

The functional trait data for the 213 bird species are presented in Appendix S2. For small-ranged species, the K values of body mass, body length and tarsometatarsus length were >1, indicating that these traits have a significant phylogenetic signal. While the other four traits have a weak phylogenetic signal, D statistics revealed that the 9 binary traits (carnivore, insectivore diets, ground foraging feeding stratum et al., see Table S5) have a significant phylogenetic signal. While the other five traits have a weak phylogenetic signal, D statistics revealed that the 7 binary traits (carnivore, insectivore diets, canopy foraging feeding stratum et al., see Table S6) have a significant phylogenetic signal, and the other 8 binary traits have a weak phylogenetic signal (Table S6).

### 3.3 Effects of environment factors on biodiversity and community structure

TD, PD and FD for the different range-size groupings appear to be influenced by different environmental factors. In the breeding season, PD and FD of total species were positively correlated with EVI. PD and FD of small-ranged species were positively correlated with MDT, STR, EVI and MTC, while PD and FD of large-ranged species were positively correlated with MDE. For TD, total and large-ranged species were positively correlated with MDE, while small-ranged species were positively correlated with MDT, STR, EVI and MTC (Table 1). In the non-breeding season, TD, PD and FD for all groupings were all positively correlated with MDT and STR and were negatively correlated with SP (Table 2).

For SES.MPD and SES.MFD in the breeding season, MDE had a negative effect on total and small-ranged species, while MDT, STR, EVI and MTC had a positive effect on large-ranged species. SES.MPD of large-ranged species was also negatively influenced by SP (Table 1). For SES.MPD in the non-breeding season, MDT, STR, EVI and MTC had a strong positive effect on large-ranged species, while SP had a negative effect on large-ranged species. SES.MFD for all range–size groupings were not correlated with any factors (Table 2).
DISCUSSION

4.1 Similarity among diversity metrics

In our study, for all range-size groupings and in the breeding and non-breeding seasons, elevational patterns of TD, PD and FD showed similar hump-shaped patterns and peaking at similar elevations within each grouping (see Figure 4). The observed similarities among diversity metrics differ from many previous studies (Jarzyna et al., 2021; Kluge et al., 2011; McCain, 2009; Montano-Centellas et al., 2019). These studies found that the probability of adding evolutionarily distinct lineages (PD) and/or species with new ecological attributes (FD) to a community assemblage decreases as assemblages become more species rich (TD). These studies also found differential loss of species from particular families and the differential loss of entire families with increasing elevation, which we did not find, shifting peaks of PD and FD to the lower elevations than TD. Our findings do not negate concerns regarding reliance on TD alone to inform conservation decisions, but they do highlight a localized pattern where the different diversity metrics show congruence. One possible explanation for the congruence we observe among TD, PD and FD is that middle elevations in the region have been important for promoting and maintaining diversity through glacial cycles and climatic fluctuations (Wu et al., 2017), which has resulted in high endemism and evolutionary distinctness at middle elevations. Middle elevations thus harbour not only increased species richness but also phylogenetic and functional distinctness.

4.2 The impacts of range size and seasonality on avian diversity and community structure

In the breeding season, we found that elevational diversity patterns for small-ranged species (elevation specialists) are skewed towards lower elevations than large-ranged species (elevation generalist), which is consistent with other studies of birds and mammals (He et al., 2019; Sun et al., 2020; Wu, Colwell, et al., 2013; Wu, Yang, et al., 2013). We do not see the same elevational skew in diversity patterns between small- and large-ranged species in the non-breeding season. As expected, however, we also documented reduced diversity in the non-breeding season across all diversity metrics, which reflects seasonal movements downslope or migration to southern latitudes for non-breeding months to escape harsh alpine winters.

The breeding-season skew in elevational diversity patterns between small- and large-ranged species might be explained by differences in ecological niche breadth. For example, larger elevational ranges are associated with a wider breadth of environmental
| Parameter       | Factors                      | Land area | SP  | MDT | STR | EVI | MDE | MTC |
|-----------------|------------------------------|-----------|-----|-----|-----|-----|-----|-----|
| PD (Total-species) | Estimate                     | 315.4     | -188.7 | 254.2 | 324.4 | 371 | 322.7 | 304.2 |
|                 | $r^2$                        | 0.442     | 0.158 | 0.287 | 0.468 | 0.612 | 0.463 | 0.411 |
|                 | $p$                          | .072      | .329 | .171 | .061 | .022 | .063 | .087 |
| PD (Small-ranged species) | Estimate                   | 294.1     | -307.7 | 335.3 | 382.54 | 516.75 | 161.7 | 363.93 |
|                 | $r^2$                        | 0.448     | 0.491 | 0.583 | 0.758 | 0.9 | 0.136 | 0.686 |
|                 | $p$                          | .069      | .053 | .028 | .005 | <.001 | .37 | .01 |
| PD (Large-ranged species) | Estimate                  | 70.51     | 71.86 | -8.592 | 22.73 | 35.11 | 204.94 | 19.93 |
|                 | $r^2$                        | 0.109     | 0.113 | 0.002 | 0.011 | 0.027 | 0.922 | 0.009 |
|                 | $p$                          | .424      | .415 | .925 | .802 | .697 | <.001 | .826 |
| FD (Total-species) | Estimate                     | 0.487     | -0.382 | 0.447 | 0.545 | 0.625 | 0.427 | 0.52 |
|                 | $r^2$                        | 0.454     | 0.278 | 0.382 | 0.568 | 0.747 | 3.481 | 0.516 |
|                 | $p$                          | .067      | .197 | .102 | .031 | .006 | .124 | .044 |
| FD (Small-ranged species) | Estimate                   | 0.434     | -0.501 | 0.542 | 0.607 | 0.654 | 0.205 | 0.591 |
|                 | $r^2$                        | 0.414     | 0.552 | 0.646 | 0.811 | 0.942 | 0.092 | 0.767 |
|                 | $p$                          | .241      | .003 | <.001 | <.001 | .012 | .963 | <.001 |
| FD (Large-ranged species) | Estimate                  | 0.213     | 0.125 | 0.006 | 0.082 | 0.122 | 0.485 | 0.073 |
|                 | $r^2$                        | 0.162     | 0.061 | <0.001 | 0.027 | 0.058 | 0.922 | 0.021 |
|                 | $p$                          | .298      | .556 | .977 | .7 | .564 | <.001 | .732 |
| TD (Total-species) | Estimate                     | 17.745    | -11.031 | 12.526 | 16.65 | 19.084 | 21.142 | 15.703 |
|                 | $r^2$                        | 0.411     | 0.347 | 0.205 | 0.362 | 0.476 | 0.584 | 0.322 |
|                 | $p$                          | .087      | .125 | .26 | .115 | .058 | .027 | .142 |
| TD (Small-ranged species) | Estimate                   | 12.771    | -11.031 | 12.617 | 14.921 | 16.613 | 9.253 | 14.211 |
|                 | $r^2$                        | 0.465     | 0.347 | 0.453 | 0.634 | 0.786 | 0.244 | 0.575 |

(Continues)
| Parameter | Factors | \( p \) | \( r^2 \) | \( p \) |
| --- | --- | --- | --- | --- |
| Land area | \( \text{SP} \) | .063 | .0162 | .323 |
| MDT | .125 | .067 | .365 | .98 |
| STR | .018 | -.009 | .741 | .98 |
| EVI | .003 | 1.729 | .83 | .98 |
| MDE | .214 | 2.471 | .36 | .98 |
| MTC | .029 | 11.825 | .71 | .98 |

**TD (Large-ranged species)**

| Estimate | \( r^2 \) | \( p \) |
| --- | --- | --- |
| 4.973 | .063 | .0162 |
| 3.614 | .067 | .323 |
| -.009 | -.001 | .98 |
| 1.729 | .02 | .741 |
| 2.471 | .04 | .98 |
| 11.825 | .916 | .98 |
| 1.492 | .001 | .98 |

**SES.MPD (Total-species)**

| Estimate | \( r^2 \) | \( p \) |
| --- | --- | --- |
| 0.05 | .001 | .931 |
| -0.96 | 0.482 | .931 |
| 0.658 | .222 | .931 |
| 0.493 | .375 | .931 |
| 0.416 | .459 | .931 |
| -1.111 | .012 | .931 |
| 0.467 | .776 | .931 |

**SES.MPD (Small-ranged species)**

| Estimate | \( r^2 \) | \( p \) |
| --- | --- | --- |
| 0.092 | .006 | .857 |
| -0.843 | 0.455 | .857 |
| 0.445 | .37 | .857 |
| 0.328 | .516 | .857 |
| 0.347 | .49 | .857 |
| -0.919 | .012 | .857 |
| 0.288 | .776 | .857 |

**SES.MPD (Large-ranged species)**

| Estimate | \( r^2 \) | \( p \) |
| --- | --- | --- |
| 0.117 | .057 | .569 |
| -0.399 | 0.303 | .569 |
| 0.433 | .01 | .569 |
| 0.408 | .041 | .569 |
| 0.355 | .307 | .569 |
| -0.203 | .017 | .569 |
| 0.393 | .776 | .569 |

**SES.MFD (Total-species)**

| Estimate | \( r^2 \) | \( p \) |
| --- | --- | --- |
| -0.195 | .021 | .733 |
| -1.018 | 0.57 | .733 |
| 0.77 | .326 | .733 |
| 0.645 | .229 | .733 |
| 0.584 | .188 | .733 |
| -1.063 | .022 | .733 |
| 0.646 | .231 | .733 |

**SES.MFD (Small-ranged species)**

| Estimate | \( r^2 \) | \( p \) |
| --- | --- | --- |
| -0.489 | .077 | .505 |
| -0.92 | 0.273 | .505 |
| 0.417 | .015 | .505 |
| 0.213 | .009 | .505 |
| 0.167 | .019 | .505 |
| -1.593 | .021 | .505 |
| 0.252 | .731 | .505 |

**SES.MFD (Large-ranged species)**

| Estimate | \( r^2 \) | \( p \) |
| --- | --- | --- |
| 0.595 | .0245 | .212 |
| -.697 | 0.336 | .132 |
| 0.895 | .555 | .132 |
| 0.998 | .689 | .132 |
| 1.028 | .731 | .132 |
| 0.445 | .137 | .132 |
| 0.942 | .614 | .132 |

Note: \( r^2_{\text{adj}} \) is the adjusted \( r^2 \) value for multiple regressions. Negative relationships are indicated by “–”. Numbers in bold indicate significant \( r^2 \) values (\( p < .05 \)).

Abbreviations: FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity; SES.MFD, the standardized effect size (SES) of the mean functional distance; SES.MPD, the standardized effect size of mean phylogenetic distances; SP, Seasonal precipitation; MDT, mean daily temperature; STR, seasonal temperature range; EVI, enhanced vegetation index; MDE, the mid-domain effect; MTC, mean temperature of the coldest month.
| Parameter | Factors  | Land area | SP | MDT | STR | EVI | MDE | MTC |
|-----------|----------|-----------|----|-----|-----|-----|-----|-----|
| PD (Total-species) | Estimate | 205 | -498.6 | 464.3 | 489.3 | 401.3 | -37.37 | 443.3 |
| $r^2$ | 0.36 | 0.765 | 0.663 | 0.737 | 0.496 | 0.004 | 0.605 |
| $p$ | .154 | .01 | .026 | .013 | .078 | .889 | .04 |
| PD (Small-ranged species) | Estimate | 205 | -296.57 | 285.09 | 292.99 | 234.4 | -36.52 | 267.35 |
| $r^2$ | 0.36 | 0.754 | 0.697 | 0.736 | 0.471 | 0.011 | 0.612 |
| $p$ | .154 | .011 | .02 | .014 | .089 | .82 | .037 |
| PD (Large-ranged species) | Estimate | 235.45 | -282.83 | 230.05 | 273.8 | 222.3 | 6.405 | 241.91 |
| $r^2$ | 0.515 | 0.743 | 0.633 | 0.696 | 0.459 | <0.001 | 0.543 |
| $p$ | .07 | .013 | .032 | .02 | .095 | .967 | .059 |
| FD (Total-species) | Estimate | 0.813 | -1.019 | 0.938 | 0.995 | 0.802 | -0.015 | 0.887 |
| $r^2$ | 0.473 | 0.742 | 0.63 | 0.708 | 0.46 | <0.001 | 0.562 |
| $p$ | .088 | .013 | .033 | .018 | .094 | .979 | .052 |
| FD (Small-ranged species) | Estimate | 0.447 | -0.624 | 0.594 | 0.615 | 0.503 | -0.085 | 0.565 |
| $r^2$ | 0.395 | 0.767 | 0.696 | 0.747 | 0.498 | 0.014 | 0.63 |
| $p$ | .131 | .01 | .02 | .012 | .076 | .799 | .033 |
| FD (Large-ranged species) | Estimate | 0.694 | -0.829 | 254.6 | 0.795 | 0.622 | 0.084 | 0.684 |
| $r^2$ | 0.5 | 0.713 | 0.602 | 0.655 | 0.401 | 0.007 | 0.485 |
| $p$ | .076 | .017 | .04 | .028 | .127 | .855 | .082 |
| TD (Total-species) | Estimate | 18.931 | -24.776 | 24.401 | 25.274 | 21.843 | 7.424 | 23.554 |
| $r^2$ | 0.45 | 0.772 | 0.748 | 0.803 | 0.6 | 0.069 | 0.697 |
| $p$ | .068 | .004 | .006 | .003 | .024 | .529 | .01 |
| TD (Small-ranged species) | Estimate | 7.513 | -10.413 | 9.819 | 10.193 | 8.268 | -0.629 | 9.181 |
| $r^2$ | 0.395 | 0.758 | 0.674 | 0.727 | 0.478 | 0.003 | 0.59 |

(Continues)
| Parameter                  | Factors | Land area | SP | MDT | STR | EVI | MDE | MTC |
|----------------------------|---------|-----------|----|-----|-----|-----|-----|-----|
| p                          |         | .131      | .011| .024| .015| .085| .911| .044|
| TD (Large-ranged species)  | Estimate| 10.825    | -13.665| 11.504| 13.894| 12.122| 4.244| 12.94|
| r²                         |         | .488      | .777| .643| .804| .612| .075| .697|
| p                          |         | .054      | .004| .03 | .003| .022| .512| .01 |
| SES.MPD (Total-species)    | Estimate| -0.43     | 1.043| -0.88| -0.965| -0.883| 0.102| -0.917|
| r²                         |         | .12       | .705| .502| .604| .506| .007| .545|
| p                          |         | .446      | .018| .075| .04 | .073| .861| .058|
| SES.MPD (Small-ranged species) | Estimate | 0.403 | -0.106| 0.16 | 0.148| 0.044| 0.03 | 0.15 |
| r²                         |         | .223      | 0.015| 0.035| 0.03 | 0.003| 0.001| 0.031|
| p                          |         | .285      | .792| .688| .711| .912| .941| .707|
| SES.MPD (Large-ranged species) | Estimate | -0.504 | 0.79 | -0.715| -0.762| -0.631| 0.028| -0.722|
| r²                         |         | .353      | 0.867| 0.709| 0.805| 0.552| 0.001| 0.723|
| p                          |         | .159      | .002| .018| .006| .056| .943| .015|
| SES.MFD (Total-species)    | Estimate| -0.266    | 0.528| -0.398| -0.458| -0.411| -0.054| -0.435|
| r²                         |         | 0.092     | 0.36 | 0.206| 0.272| 0.219| 0.004| 0.245|
| p                          |         | .509      | .154| .307| .23 | .289| .897| .258|
| SES.MFD (Small-ranged species) | Estimate | 0.106 | 0.009| 0.158| 0.101| 0.159| -0.532| 0.166|
| r²                         |         | 0.01      | <0.001| 0.022| 0.009| 0.022| 0.25 | 0.024|
| p                          |         | .832      | .985| .751| .84 | .749| .253| .739|
| SES.MFD (Large-ranged species) | Estimate | 0.839 | -0.66| 0.47 | 0.575| 0.349| 0.625| 0.462|
| r²                         |         | 0.499     | 0.309| 0.157| 0.234| 0.086| 0.277| 0.151|
| p                          |         | .076      | .195| .38 | .271| .523| .225| .389|

Note: $r^2_{\text{adj}}$ is the adjusted $r^2$ value for multiple regressions. Negative relationships are indicated by "-". Numbers in bold indicate significant $r^2$ values ($p < .05$)

Abbreviations: FD, functional diversity; PD, phylogenetic diversity; TD, taxonomic diversity; SES.MFD, the standardized effect size (SES) of the mean functional distance; SES.MPD, the standardized effect size of mean phylogenetic distances; SP, Seasonal precipitation; MDT, mean daily temperature; STR, seasonal temperature range; EVI, enhanced vegetation index; MDE, the mid-domain effect; MTC, mean temperature of the coldest month.
conditions, which is assumed to be associated with increased environmental and physiological tolerance in animals (Slatyer et al., 2013; Wu, Colwell, et al., 2013). Given this increased breadth of environmental conditions and physiological tolerance in large-ranged species, we would expect factors other than environmental conditions to disproportionately impact range limits, such as spatial factors like geometric boundary constraints (Colwell et al., 2004). Our findings support this scenario. That is, for large-ranged species, we find that spatial factors, like the mid-domain effect, best explain elevational diversity patterns. In contrast, diversity patterns for small-ranged species, which presumably occupy a narrower environmental niche space, are best explained by climatic variables (like mean daily temperature, seasonal temperature range and mean temperature of coldest month) and productivity variables (like enhanced vegetation index; Table 1, Figure 3).

In the non-breeding season, however, elevational patterns for all diversity metrics are similar between small- and large-ranged species groupings and shift to lower elevations. We found that these diversity patterns are best explained by climatic variables (like seasonal precipitation, mean daily temperature and seasonal temperature range), suggesting that climatic variables, particularly during seasonally harsh montane winters, disproportionately shape elevational range limits and elevational patterns of diversity, rather than spatial factors like the mid-domain effect.

We also found that phylogenetic and functional community structure varied between elevational range-size groupings. In the breeding season, for small-ranged species, both community structure metrics showed trends of overdispersion at low and high elevations, clustering at middle elevations, which is inconsistent with previous studies (Hanz et al., 2019; He et al., 2018; Montano-Centellas et al., 2019). While we cannot explain the ecological basis of these patterns given our environmental data (including productivity), we found evidence for the loss of functionally redundant species at low and high elevations, which would lead to patterns of functional overdispersion at these elevations. Although low and high elevations have fewer species, most of the main functional guilds of birds remain present in these habitat (Figure S7), increasing the average distance between species in trait space. For small-ranged species, we also found evidence for loss of sister taxa at low and high elevations, but not a loss of the entire clades—that is, we found a higher rate of decline in species from middle elevations to low and high elevations than that of families and orders (Table S7). These data suggest that within-clade competition increases at low and high elevations (Srinivasan et al., 2018), which would lead to patterns of phylogenetic overdispersion.

Small-ranged species showed similar trends in community structure between seasons. However, patterns of community structure were far more irregular in the non-breeding season (Figure 4), which is likely explained by the lack of species at upper elevations during this period. The vast majority of small-ranged species occur at low elevations in the non-breeding season. We only record three species (2 Families) at 3200–3599 m and 3600–3999 m elevations, respectively (Table S7).

For large-ranged species in the breeding season, functional and phylogenetic community structure showed trends of clustering as elevations increased. However, phylogenetic community structure was more clustered than functional community structure, which we would expect if habitat filtering becomes increasingly important at upper elevations as climate becomes harsher and productivity decreases (e.g. see MDT, STR and EVI in Figure 3). This dynamic may limit the lineages that have historically been able to occupy a given environment (Dreiss et al., 2015; Hanz et al., 2019; Montano-Centellas et al., 2019). Patterns of phylogenetic and functional community structure for large-ranged species, however, shift in the non-breeding season, with community structure becoming more less clustered and more overdispersed and/or even at upper elevations, which is consistent with a hypothesis of increased interspecific competition (the highest three elevation bands are excluded because of few species present). These seasonal differences in community structure could be explained by the dramatic differences in food availability between seasons in temperate mountain regions. For example, during breeding months when resources are abundant, habitat filtering appears to be important in defining community structure, but when resources are scarcer during non-breeding months, competition shapes community structure. That is, species that are functionally and phylogenetically distinct (i.e. overdispersed) are less likely to compete for similar resources and are thus more likely to co-occur in non-breeding months (Figure S8).

When we assess range-size grouping together (total species), elevational patterns of community structure varied between breeding and non-breeding seasons. At low elevations, functional and phylogenetic community structures are broadly more clustered in the non-breeding season, which suggests a reduced impact of interspecific competition and an increased impact of habitat filtering during non-breeding months. This pattern might be explained by two interacting factors: (1) departure of migratory species decreases local species richness in the non-breeding season and subsequently decreases interspecific competition; and (2) more reproduction-based resources are needed in the breeding season, thus increases interspecific competition for these resources. At middle and high elevations, functional and phylogenetic community structures are broadly more overdispersed in the non-breeding season, which further supports findings of overdispersion in regions with low resource availability and harsh environmental conditions (Brun et al., 2019; Spasojevic & Suding, 2012). These findings are somewhat counter-intuitive given that harsh environmental condition are often thought to be associated with habitat filtering, but when paired with low resource availability and seasonality, a large portion of the avifauna migrates away from these environments in the non-breeding season when competition for resources would increase. Thus, we would expect that species that remain would overlap less in their feeding ecology.

Taken together, these findings highlight the complexity of biodiversity distributions, and how the factors that shape patterns of diversity and community structure often shift along environmental
gradients (like elevational gradients) and through time (like across the annual cycle). Accounting for seasonality can help us better understand the mechanisms that drive community structure and diversity patterns as resources, environmental conditions, and community composition shift across the year.

### 4.3 The implications of seasonality for biodiversity conservation

Birds are indispensable to mountains ecosystem as seed dispersers and pollinators and as predators and prey, shaping the ecological community (Sekercioglu et al., 2016). Both large- and small-bodied species showed highest diversity (across all three diversity metrics) at mid-elevations in the breeding season, suggesting areas of conservation priority that harbour high species richness, evolutionary distinctness and functional diversity. Middle elevations in this region have also been shown to harbour high endemism and mammal diversity (Wu et al., 2017; Wu, Yang, et al., 2013). However, in the non-breeding season, lower elevations become important havens for species that over-winter in the region, which requires conservation attention as these elevations are experiencing far more human disturbance than upslope. Our study highlights how seasonality is an important dimension in shaping community structure across the annual cycle of an ecosystem. Previous research on long-distance migrants, for example, has shown the importance of non-breeding distributions for species conservation (Martin et al., 2007; Norris et al., 2004). This work has brought increasing attention to non-breeding distributions. However, instead of assessing seasonal distributions for individual species, we have taken a community approach, studying seasonal processes that shape community structure in a given place over the course of the year. Taken together, our findings, along with previous work on individual species, highlight how accounting for the entire annual cycle of a place (or a species) is critical to inform conservation and land-use strategies.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.
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**BIOSKETCH**

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