Trait-mediated filtering drives contrasting patterns of species richness and functional diversity across montane bird assemblages

Qiang Zhang1 | Marcel Holyoak2 | Chuanwu Chen3 | Zhifa Liu4 | Jiajia Liu5 |
Xianli Che1 | Anqiang Dong6 | Changteng Yang4 | Fasheng Zou1

Abstract

Aim: Most studies of diversity changes along elevational gradients show a synchronous change in taxonomic, functional and phylogenetic diversity, such that all decline with elevation or show a mid-elevation peak. However, some studies show asynchronous changes, which challenge us to explain their assembly. Here we used functional trait variation and niche spacing to test the roles of environmental filtering and competition-driven niche separation in assembly and biodiversity patterns across an elevational gradient.

Location: Nanling Mountains, southern China.

Taxon: Birds (Timaliidae, Pycnonotidae and Sylviidae)

Methods: Breeding birds were surveyed in 2012–2017 from 300 to 1900 m ASL. We tested bird diversity pattern and community structure relevant to environmental filtering and limiting similarity by integrating functional traits and evolutionary distances, as well as vegetation heterogeneity. A null modelling approach tested specific trait variation and niche spacing in relation to habitat associations and niche segregation.

Results: Contrary to expectation, bird richness peaked at just below the highest site, and functional diversity declined significantly with elevation. Functional–phylogenetic distance metrics converged with increasing elevation, corresponding to strong environmental filtering and habitat change. For the spatial arrangement of specific traits, restricted dispersal ability, elevational range and clutch sizes were related to filtering effects, as indicated by trait convergence in clustered highland bird assemblages. Conversely, overdispersed lowland assemblages have evenly spaced trait values predicted by limiting similarity, including bill length, vertical stratum-use and flocking propensity. In addition, bird functional diversity was highly correlated with both vegetation productivity and tree height, which reinforces the role of filtering in structuring local bird assemblages.

Main conclusions: This study highlights how strong filtering can produce a counter-intuitive, contrasting pattern of changes between species richness and functional diversity. Fundamental assembly processes and species roles in ecosystems are predictable through examining key traits of life-history and foraging characteristics, and their associations with environmental variables.
1 | INTRODUCTION

Disentangling the processes that shape community assembly, species diversity and distributions across elevational gradients remains a fundamental challenge in ecology (Graham et al., 2014; Quintero & Jetz, 2018). Elevation gradients provide dramatic turnover along biotic clines and climatic conditions over short geographical distances, and often contain many narrowly distributed species that are threatened by habitat modification and climate change (Lomolino, 2001). A natural question that arises is whether multiple facets of diversity act as surrogates for each other. However, several studies have found a lack of surrogacy across various spatiotemporal scales which challenge us to explain their assembly, because of lack of concordance in different habitat constraints, biotic interactions, dispersal limitation and evolutionary history (Bässler et al., 2016; Purschke et al., 2013). Consequently, an integrative evaluation of variation in multiple diversity is needed to obtain a holistic view of montane community assembly, since it remains unclear whether assembly processes act independently, interactively or sequentially. In addition, studies of the distributions of species and diversity have re-emerged with new urgency, as species identity alone (e.g. species richness or taxonomic diversity) is not sufficient to infer a deeper mechanistic understanding of the underlying assembly processes (Jarzyna & Jetz, 2016). A growing interest to elucidate patterns of species assembly and biodiversity effects on ecosystem services has boosted the development of methods and studies focusing on species’ ecological and life-history differences (Bello et al., 2017; McGill, Enquist, Weiher, & Westoby, 2006).

Mechanistic models of community assembly state that biotic and abiotic filters constrain where species live and how they interact through selection on their functional traits (Perronne, Munoz, Borgy, Reboud, & Gaba, 2017). Quantifying the response of trait dispersion patterns to environmental changes has enhanced our understanding of key ecological processes that structure communities (Aiba et al., 2013; Kraft & Ackerly, 2010). Our study employ the deterministic framework of trait-based niche theory, which assumes that differences in functional signatures (i.e. phenotypic attributes) can be linked to the relative fitness of coexisting species along elevational gradients (Graham, Parra, Tinoco, Stiles, & McGuire, 2012; Viole et al., 2007). Such approaches predict contrasting patterns in the co-occurrence of species with particular functional traits, based on environmental filtering or limiting similarity (Table 1: Table S1 in Appendix S1). For instance strong abiotic filters are expected to constrain the range or variance of species trait values leading to convergent trait distributions, such as a lower functional divergence, and a higher functional overlap (Cornwell, Schwilk, & Ackerly, 2006). The limiting similarity principle postulates that under resource limitation, competition leads to niche differentiation represented by a divergent distribution of trait values. Competing species can therefore only coexist if they differ in their traits, such as a higher functional divergence and a more regular spacing of trait values (Weiher & Keddy, 1995). However, the ‘weaker competitor exclusion’ may also cause strong trait convergence at relatively small scales where only strong competitive traits are retained. The pattern is mostly expected for plant traits related to the use of a limiting resource, such as light in highly productive environments (Mayfield & Levine, 2010). Here we predict that different assembly processes operate simultaneously to structure local communities, and their relative importance may change along elevational gradients.

Studies suggest that multiple-niche-axis metrics may produce misleading evidence that niche-based processes are partitioned, which highlight the importance of analysing functional assembly models using single-niche-axis (Trisos, Petchey, & Tobias, 2014). For instance multiple assembly processes operate simultaneously to structure communities along a stress-resource gradient. These processes would be obscured by a single multivariate trait index or phylogenetic diversity and are only evident by analysing functional diversity patterns of individual traits (Spasojevic & Suding, 2012). One limited reason for the use of multiple traits is that identifying filtering—and competition-related traits a priori can be challenging. While species interactions related to a particular resource or niche always contribute to community structure to some degree, no single niche may act separately (Lopez et al., 2016). Thus, the use of multivariate metrics or phylogeny might obscure overlapping niche-based processes that would be more apparent if traits are considered separately (Aiba et al., 2013; Lasky et al., 2014). A further complication is that most studies have relied on the niche conservatism assumptions that phylogenetic similarity reflects ecological similarity (e.g. as indicated by morphological convergence) and that close relatives are strong competitors (Lovette & Hochachka, 2006; Wiens et al., 2010). However, rapid evolution in response to factors other than limiting similarity or environmental filtering may also produce either convergent or divergent patterns of phylogenetic relatedness (Cadotte, Albert, & Walker, 2013). Lastly, traits may be labile in response to environmental or ecological conditions (Loughman & Gilbert, 2017; Savage & Cavender-Bares, 2012). As such, we argue that specific traits conferring changes in fitness with elevation are likely to provide stronger evidence about the relative importance of abiotic and biotic assembly processes.

With well-known life histories and phylogenetic relationships, forest birds in mountains facilitate us to understand how species response to elevational gradients (Barnagaud et al., 2014; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Bird traits that respond to elevational stressors include those relating to variation in foraging (e.g. dietary adaptations, habitat preferences and sociality), breeding, morphology associated with dispersal ability and elevational range (see Appendix S1). Meta-analyses have documented

KEYWORDS

community assembly, environmental filtering, limiting similarity, Nanling Mountains, niche conservatism, trait convergence
of trait-based assembly, we assumed that competition-related traits are seldom tested using specific traits that relate to individual community assembly processes (except for body size). In the framework of trait-based assembly, we assumed that competition-related traits included those associated with behaviour, microhabitat specialization or resource acquisition, and led to niche differentiation by allowing species to partition available resources (Lovette & Hochachka, 2006). In addition, filtering-related traits were those that provided tolerance to environmental conditions (such as temperature or precipitation) or determined species positions along environmental gradients (Lopez et al., 2016). Lowlands generally have higher resources abundance and more appropriate microclimate than highlands counterpart. Thus, we predict that environmental tolerance in harsh high elevations would have resulted in decreased trait range or variance, causing trait convergence towards a single optimum (Graham et al., 2012). In the lowlands, limiting similarity is postulated to allow coexistence through limited between-species niche overlap, creating an even pattern of trait divergence because species with overlapping resource requirements could be excluded by competition (Table 1, Figure 1a). It also leads us to predict that elevational patterns between taxonomic and functional diversity can be represented by four idealized states (Figure 1b-e, see Appendix S1 for details).

Here we focus on the association between environmental filtering, functional traits and evolutionary history of elevational forest birds, extending the findings to montane assembly by accounting for species’ ecological differences. By evaluating the power of multiple-niche-axis (including phylogeny) and single-niche-axis metrics, we tested three hypotheses: (a) Elevation gradients will produce changes of the congruent sign in species richness and functional diversity, and these changes will be correlated with environmental factors indicated by vegetation heterogeneity. (b) Trait-mediated filtering will select for sets of closely related species with decreased trait variance at high elevations, whereas competitive exclusion will favour more distinct species and evenly spaced trait values in lowlands. (c) Key ecological and life-history traits will contribute to community composition and ecosystem function. Filtering-related traits provide tolerance in harsh environments, whereas competition-related traits are expected to be associated with resource partitioning.

2 | MATERIALS AND METHODS

2.1 | Study site and field data collection

The Nanling or ‘Southern’ Mountains are the third-most important biodiversity ecoregion in China, and occupy the easternmost boundary of Sino-Japanese and Oriental realms. The mountain ranges are situated between 110°-117°E and 22°40'-26°20' N, straddling...
over 1,000 km from west to east. They represent an important boundary between the south and central subtropical zones, and define the watersheds of the Yangtze and Pearl Rivers. Our survey was conducted along the south slope of Nanling National Nature Reserve, which is in the central part of the Nanling Mountains covering 584 km² (Figure S1 in Appendix S1). Shikengkong summit represents a high point at 1,902 m. The region has a subtropical monsoon climate, with a mean annual temperature of 17.4°C. Annual precipitation ranges from 1,570 to 1,800 mm, and mainly occurs between March and August. The elevational gradient of vegetation communities encompasses mountain broadleaved evergreen forest, mixed evergreen and deciduous forest, coniferous and broadleaved mixed forest, montaintop dwarf forest and montane shrubs and herbs.

Bird communities were sampled twice yearly during the breeding season (April–July, from 2012 to 2017) at 16 forested elevational sites (100-m vertical intervals from 300 to 1900 m ASL). Sampling used fixed line-transect and point-count methods (Zhang, Han, & Zou, 2011). Each site was sampled using 2.5-km transects along existing trail networks, with 10 permanent survey points spaced along each transect. In each survey, two observers walked together along each transect at a constant speed (c. 2.0 km/hr), and recorded all the birds detected by either visually oraurally. Meanwhile, timed point-count was conducted for 10 min within a 25 m radius plot. We also recorded species’ vertical substrates (air, canopy, trunk, understory, ground) and activity (calling, flying, perching, foraging, nesting, flocking) for bird guild analyses. Censuses were initiated on windless and rainless days at sunrise and terminated before 10:30 a.m. Nocturnal raptors, water birds, aerial feeders and non-breeding migrants were excluded in the study. Our analyses used records of richness and abundance of each species accumulated through the 6-year period, such that a species had to be entirely absent throughout the 6-year period to be recorded as absent from the site. This cumulative procedure helps reduce inter-annual variations (Table S2 in Appendix S1).

Vegetation variables were quantified along each of the bird transects. On each transect we placed ten 10 × 10 m quadrats, and measured DBH (diameter at breast height at 1.3 m above ground), and height of all tree species (woody plants with DBH >2 cm). Within each quadrat, we enumerated the density, height and coverage of shrubs (DBH <2 cm) and herbs. The importance value (IV) for each species in each quadrat was calculated as the sum of the relative frequency, density and basal area. From the abundance and richness data, we also separately calculated the Shannon–Wiener diversity index (H′) for tree, shrub and herb species for each quadrat. Moreover, remotely sensed NDVI (mean normalized divergence vegetation index) data were used as measures of primary productivity for each 100-m elevational band. One cloud-free geo-corrected Landsat-8 image (band LC81230432016061GN00) was downloaded from the Geospatial Data Cloud (GDC, at http://www.gsccloud.cn/) in Southern China. Mean NDVI values were calculated from the surface reflectance of Red and NIR bands of Landsat 8 sensors for January, April, July and October for 2013 and 2015, using ENVI 4.0.

FIGURE 1 Potential consequences of ‘environmental filtering’ and ‘limiting similarity’ hypothesis for TD (species richness), FPD (functional-phylogenetic diversity) and assembly processes along elevational gradients. The figure assumes a strong phylogenetic signal, so that functional and phylogenetic diversity are strongly and positively correlated. Effect size is a measure of the magnitude and direction of the observed spacing relative to a null expectation [Colour figure can be viewed at wileyonlinelibrary.com]
2.2 Assumption checks based on trait metrics and environmental heterogeneity

Bird trait selection and phylogeny construction are fully detailed in Tables S3 and S4; Figures S2 and S3 in Appendix S1. To illuminate the ecological assembly processes, we used a method recently proposed which is uncorrelated with local species richness but allows for an interpretation of the dominant process (random or niche-related). It integrates both the measured traits (Gower distance) and the phylogeny (patristic distance) into a single measure using the function ‘funct.phylo.dist’ in R package ‘pez’, to create the functional–phylogenetic distance matrix (FPD). This integrative approach aims to overcome the shortcomings of approaches exclusively based on FD or PD, and considers similarity among species not covered by the chosen trait set, and examines whether PD can provide complementary information to the FD based on traits only (Cadotte et al., 2013). The calculated FPD matrix measures the distance between different species, and includes a phylogenetic weighting parameter, α-value, which scales the relative contribution of FD and PD to the FPD matrix. For example when α = 0, only FD contributes to the FPD and only PD when α = 1. Otherwise, at an intermediate value of α, both of FD and PD contribute to the resulting FPD matrix. To infer community assembly mechanisms (i.e. environmental filtering vs. competitive exclusion) across elevational bird assemblages, we calculated the standardized effect size of the mean FPD (SES. MFPD) using the function ‘ses.mpd’ in R package ‘picante’. This FPD measure can be used to interpret dispersion and assembly patterns: positive SES values indicating overdispersion (e.g. filtering), and negative values indicating clustering (e.g. competition). To test for robustness of the results in relation to the MFPD measure, we separately calculated the phylogenetic and functional dispersion using Rao’s quadratic entropy (PhyRao and FunRao, respectively, see Appendix S1 for details). All metrics were expressed as SES with both abundance and incidence data, which were differences from a randomized community scaled by the standard deviation of the null community.

Because both biotic and abiotic processes can produce clustering (i.e. Table 1), we additionally analysed specific trait dispersion and habitat heterogeneity to detect potential drivers of community clustering. First, we calculated dispersion metrics for each of the continuous traits following the R script from Kraft and Ackerly (2010). To evaluate the role of filtering, we quantified the range (RANGE) and variance (VAR) of trait values, but because VAR and RANGE are highly correlated (all traits, p < .01), we retained VAR in subsequent analyses. To quantify trait spacing (Figure S4 in Appendix S1), we computed the standard deviation of nearest neighbour distances normalized to range (SDNNr, referred to as limiting similarity), by identifying the most similar co-occurring species to each successive species. Then we measured how evenly spaced traits were across the entire assemblage by quantifying the standard deviation of nearest distances along a single direction normalized to the range (SDNDr, referred to as evenness of spacing). For each bird assemblage, we calculated the observed spacing metric and the mean and standard deviation of the same metric based on 999 random assemblages by sampling species with equal probability from the regional species pool. For dispersion of specific trait metrics, we visually inspected violin plots that represent the density of data, and used standardised metrics to test for significant patterns of clustering or over-dispersion. Specifically, we tested the significance using Wilcoxon signed-rank tests. Negative effect sizes for VAR would suggest environmental filtering, while negative SDNNr and SDNDr would suggest competition-driven limiting similarity and even spacing of traits (Figure 1a). Finally, we used Pearson’s correlation to test for univariate relationships between single trait metrics and elevation as well as phylogenetic structure indices for 16 bird assemblages across elevation.

For environmental variables related to abiotic filtering, we used a principal component analysis on standardized data to visualize niche contribution within each vegetation category. Species scores on the first two axes explained 53.4% of the variance, and the seven available vegetation variables were used in subsequent analysis (Table S5 in Appendix S1). The first axis explained 33.4% of variation in vegetation data and indicated tree structure. Increasing values were associated with more forested habitat at low elevation, including increased maximum tree height and tree diversity, and decreased shrub and herb diversity. While the second axis was correlated with decreasing tree height and DBH, and a higher density of understory plants (shrubs and herbs) at high elevation. Then, we performed a canonical correspondence analysis (CCA) to test the response of breeding birds with different ecological strategies or functional traits to vegetation variables along an elevational gradient. We also tested the relationships between different diversity metrics and vegetation variables using multiple regression analyses.

2.3 Statistical analyses

To compare sampling effort and completeness of bird inventories across 16 elevational sites, we performed rarefaction analyses based on a Monte Carlo simulation procedure (1,000 runs) by R functions ‘rarefy’ in ‘vegan’ package. To examine the elevational pattern of different bird diversity metrics (TD, PD, FD and FPD), we constructed general linear models (GLMs) with identity link function and negative binomial error structure (to account for count data that could not extend below zero) for each metrics, and added species richness in all models as the continuous covariate. A second order polynomial regression were used to quantify the distribution of each metric along the elevational gradient. For each of the four categorical traits of habitat preference, diet, vertical stratum-use and social flocking, we calculated the species richness in each guild. For other continuous traits, we calculated the average value per site, weighted by local abundance. To calculate total bird biomass for each site we multiplied body mass per species by abundance. Due to the inherently interaction of continuous traits or environmental factors, we performed hierarchical clustering
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3 | RESULTS

3.1 | Multiple facets of diversity and species composition

Altogether, 16,874 individuals from 80 bird species were recorded during the breeding season for six years. The results of 16 sample-based rarefaction curves illustrated the completeness of bird inventories of each site and the sufficiency of sampling efforts, given their rapid approach to asymptote (Figure S5 in Appendix S1). Overall species richness increased nearly linearly with elevation (Figure 2a, $r = .60, p = .01$). Bird abundance did not change with elevation, whereas bird biomass (weighted by species richness) significantly decreased (Figure 2b; Figure S6 in Appendix S1). However, both Rao's PD (Figure 2c, $r = -.49, p = .05$) and multi-trait metrics of Rao's FD (Figure 2d, $r = -.71, p = .02$) decreased significantly with elevation, and PD was strongly correlated with FD ($r = .720, p = .002$). For species composition, high-elevation assemblages contained a high proportion of forest specialists, social-flocking species and understory insectivores, but a few edge-tolerant and open-habitat species (Figures S7 and S8 in Appendix S1).

3.2 | Phylogenetic and functional community structure

For community structure of bird assemblages (i.e. abundance-weighted), all of the integrated functional–phylogenetic (SES. MFPD), phylogenetic (SES.MPD) and multivariate trait metrics (SES. MFD) had negative values and decreasing trends with elevation (Figure 2f; Figure S9 in Appendix S1). For SES.MFPD, the adjusted $R^2$ value reached its maximum (0.65) when $a = 0$ (Figure 2e). This indicates the robustness of trait selection in this study, because functional distance majorly contributed to FPD. Hence, high FPD clustering indicated strong environmental filtering selecting for sets of functionally similar species at higher elevations. Conversely, biotic interactions, inferred from more dispersed functional traits, favoured more distinct species in lowlands.

3.3 | Dispersion of specific trait metrics

Average values of nine continuous traits revealed significant convergence towards high elevations (Figure S10 in Appendix S1). Negative SES values and Wilcoxon signed-rank tests for trait spacing metrics showed less variance than random assemblages. Specifically, we observed increased filtering as evidenced by dispersal ability, clutch size and flocking propensity (i.e. declining VAR accompanied by significant correlation with increasing elevation, and clustered/similar assemblages at higher elevations; Table 2; Figure S11 in Appendix S1). In contrast, we observed phylogenetic dispersion and even distribution of competition-associated characteristics of vertical stratum-use, bill length and flocking propensity at low elevations, which are related to microhabitat specialization or resource acquisition (Table 2; Figure S11 in Appendix S1). Regression models reinforced that FPD metrics were correlated with the aforementioned six filtering- and competition-related trait metrics ($R^2 < .806$; Table S6 in Appendix S1).

3.4 | Effects of environmental factors on bird diversity

Species–habitat relationships (CCA) showed an environmental effect on bird composition, corresponding to two niche-axes (Figure 3; Table S5 in Appendix S1). The first axis explained 33.4% of variation in vegetation data and indicated tree structure. Increasing values were associated with more forested habitat at low elevation, including increased maximum tree height and tree diversity, and decreased shrub and herb diversity. The second axis was correlated with decreasing tree height and DBH, and a higher density of understory plants (shrubs and herbs) at high elevation. Multiple regression models indicated that bird richness was less correlated with vegetation structure ($R^2 = .23$) than composition, and bird abundance was only associated with NDVI ($R^2 = .40$). Meanwhile, PD, FD and FPD metrics were highly correlated with the maximum size of large trees ($R^2 > .55$, Table 3).

4 | DISCUSSION

4.1 | Contrasting patterns of bird species richness and functional diversity

Previous studies provide a limited understanding of why montane species show inconsistent patterns in the multiple facets
of diversity. However, such incongruent patterns occur because local co-occurrence of species is derived by diverse ecological processes, and biogeographical and evolutionary histories (Mittelbach & Schemske, 2015). Studies typically found that multiple diversity either declined or increased with increasing elevation for most taxa (Table S1 in Appendix S1). For instance a clustered community was accompanied by synchronously decreasing TD and FPD, created by survival of species that are functionally similar and have traits conducive to survival at high elevations (Figure 1b). Studies of rodents, frugivorous birds, bees and soil bacteria have exemplified this filtering effect (Table S1 in Appendix S1), and these taxa represent a transition from competition-driven dispersion and abundant niche opportunities in mild conditions to strong filtering and limited niches in harsh environments. In contrast, we found that taxonomic richness increased with elevation and showed a high-elevation peak, whereas functional diversity decreased. Our study indicates increasing environmental selection for closely related species with certain functional traits, because of the gain of functionally redundant species (Figure 1c). This contrasting pattern has only been found in the lichen community (from 300 to 1450 m ASL, Bässler et al., 2016). In addition, we were not able to explain as much variation in PD as multivariate FD metrics (Figure S9 in Appendix S1), which illustrates the value of using functional traits to predict future diversity changes under environmental
TABLE 2 Correlation coefficients between single trait metrics and elevation as well as phylogenetic structure indices (SES MPD) for 16 assemblages across elevation

| Filtering-related traits and index | Correlation coefficient | Competition-related traits and index | Correlation coefficient |
|-----------------------------------|-------------------------|--------------------------------------|-------------------------|
|                                   | Elevation | SES MPD |                                   | Elevation | SES MPD |
| Dispersal ability                  |           |         | Vertical stratum                   |           |         |
| Mean                              | −0.604**  | 0.545*  | Mean                               | −0.595*   | 0.559*  |
| VAR                               | −0.591*   | 0.728** | VAR                                | −0.479    | 0.496   |
| SDNNr                             | 0.582*    | −0.334  | SDNNr                              | −0.005    | −0.293  |
| SDNDr                             | 0.447     | −0.356  | SDNDr                              | 0.616*    | −0.505* |
| Clutch size                       |           |         | Bill length                        |           |         |
| Mean                              | −0.511*   | 0.452   | Mean                               | −0.675**  | 0.617*  |
| VAR                               | −0.564*   | 0.683*  | VAR                                | 0.212     | −0.178  |
| SDNNr                             | −0.405    | 0.313   | SDNNr                              | −0.493    | 0.584*  |
| SDNDr                             | −0.023    | −0.046  | SDNDr                              | −0.730**  | 0.732** |
| Elevation range                   |           |         | Flocking propensity                |           |         |
| Mean                              | −0.735**  | 0.694** | Mean                               | −0.757**  | 0.697** |
| VAR                               | 0.595*    | −0.676**| VAR                                | −0.011    | 0.134   |
| SDNNr                             | 0.334     | −0.408  | SDNNr                              | −0.627**  | 0.485   |
| SDNDr                             | 0.382     | −0.400  | SDNDr                              | −0.586*   | 0.468   |

Note: The significance of correlation are indicated as bold values, *p < .05, **.001 < p < .01. p-values were adjusted for multiple comparisons using FDR (false discovery rate) procedure.
Abbreviations: SDNDr, standard deviation of the nearest distances; SDNNr, standard deviation of nearest neighbour distances; VAR, trait variance.

stress. The congruent patterns between FD and PD indicate the tendency of species to retain ancestral ecological characteristics, such that functional traits are phylogenetically conserved, except for flocking propensity and breeding period (e.g. niche conservatism, Wiens et al., 2010).

4.2 | Mechanisms inferred from multivariate indices and environmental factors

Integrating functional and phylogenetic distances highlights a powerful approach to reveal underlying mechanisms in shaping community structure (Cadotte et al., 2013). At high elevations of Nanling Mountains, selection for sets of functionally similar bird species resulted in functional clustered patterns (Figure 2f). Whereas increased biotic interactions and niche opportunities (e.g. plant species richness) likely favoured more distinct species at lower sites. The observed decline of difference in SES.MFPPD with elevation is consistent with previous studies of soil bacteria, hummingbirds, ants, bees and lichens (Table S1 in Appendix S1). In contrast, some studies on plant communities, Himalayan leaf warblers and bat assemblages, found that the difference in dispersion from null communities increased with elevation (Table S1 in Appendix S1). A possible explanation is that the threshold to the environmental filtering may vary between species taxa (Bryant et al., 2008), or some traits which are not phylogenetically conserved (e.g. skull length and wing aspect-ratio of bats, Cisneros et al., 2014). Clustering bird assemblages may be attributed to strong abiotic filtering effect, whereby the low temperatures, strong seasonality and increasingly shrubby plant communities select for a specific combination of conserved traits with adaptive characteristics. For instance a larger proportion of understory insectivores (e.g. laughingthrushes, parrotbills, shortwings and bush warblers) and canopy flocking species (e.g. leaf warblers, shrike babblers) were restricted to elevations above 1,000-m ASL in Nanling Mountains (Figure 3a, b). The restricted taxonomic groups (and functional clustering) at high elevations are consistent with the fact that those species have ancestral characteristics, allowing them to colonize and persist in cold climates. In Himalayan leaf warblers, Ghosh-Harilhar (2014) found that beak shape may be an adaptation of competitively species to potentially stressful high-elevation environments. Similarly, Graham et al. (2012) found phylogenetic clustering in the high-elevation Andean hummingbird communities and suggested that it reflected niche-conserved adaptations to low temperature stress.

The strong filtering effect was reinforced by relationships between vegetation factors and bird composition. First, CCA ordination and regression models revealed that variations in vegetation variables were divided into two niche-axes, representing the frequency of large trees/PC1 and dense understory shrubs and herbs/PC2 (Figure 3; Table S5 in Appendix S1). This is in line with the classic view that bird species diversity could be predicted from the mean foliage profile of the habitat or proportional to foliage height diversity (MacArthur & MacArthur, 1961). In addition, while variation in mountain climate has been related to species richness of plants and ectothermic animals through the ‘physiological tolerance hypothesis’, it directly influences community composition of endotherms such as birds mostly under stressful climatic conditions (Ferger, Schleuning,
NDVI indicate decreased competition at high elevations. A decrease in competition might increase the role of niche-related processes and environmental attributes in community assembly. Lastly, FPD metrics were correlated with both NDVI and large trees (high DBH and height), implying that multi-level filtering determines the functional composition of bird assemblages (Sydeman, Moe, Totland, & Eldegaard, 2015). Altitude together with vegetation factors were related to changes of species assemblages in functional distance, which suggested that the relative importance of environmental factors varied across the elevational gradients, and specific alpha and beta traits determine which species pass through the environmental filters individually.

### 4.3 Assembly processes inferred from variation in specific traits

The dispersion of the specific trait metrics provides further insights into the major biological mechanisms acting along the elevational gradients. Univariate traits of clutch size, elevational range and dispersal ability showed obvious elevation declines of both mean community values and VAR (Table 2). These ecological and life-history trait responses to filtering include a combination of temperature constraints on elevational range and similarity in fecundity that potentially yield high fitness in cold, high-elevation sites. For breeding characteristics, elevational variation in life-history traits has been attributed to four major environmental stresses: nest predation, food limitation, breeding phenology and climate (Badyaev & Ghalambor, 2001). We found that high-elevation species had a shorter breeding season and smaller clutch size than low-elevation species. Although mean values changed in tests of trait variance, only clutch size had a significantly lower variance compared to random assemblages for single-trait metrics. Several observations indicate strong climatic effects on the phenology of breeding in high-elevation species. Badyaev (1997) reported that 23 pairs of closely related finches had smaller clutches, fewer broods and longer incubation periods, which contributed to a trade-off between greater juvenile survival and reduced fecundity. In our study, shorter breeding seasons, colder climate and lower diversity of tree species could account for the smaller clutch size with low variance in high-elevation birds. Moreover, upland species also had narrower elevational range with low VAR. Species’ range is determined by complex interactions among multiple factors, including physiological tolerance, life-history traits, behavioural plasticity and history of speciation and dispersal (Jetz & Rahbek, 2002). We therefore believe that our findings are largely explained by the long-standing theory that abiotic factors commonly set range limits in stressful environments of higher latitudes (Louthan, Doak, & Angert, 2015). For example strong patterns of species turnover along elevational gradients, and habitat specialization arising from particular requirements for foraging or reproduction may narrow the range of resources a species can utilize efficiently and thereby enforce range limits (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008). Similarly, filtering-related traits reflecting dispersal ability (i.e. wing length and body mass) are expected to relate to a species’ degree of

**FIGURE 3** Canonical correspondence analysis (CCA) on community composition of (a) sampling sites scores, and (b) bird species scores. Arrows refer to environmental variables (Table S5), and distance and angle of species scores from the center point on the plot indicate strength of environmental preferences. Refer to Table S2 for site codes and abbreviation of birds (site colour represent gradient for count of bird species richness from green/low to blue/high, species colour represent different families same as Figure S8) [Colour figure can be viewed at wileyonlinelibrary.com]
specialization or tolerance, and should be particularly important in shaping metacommunity structure. In our study, short breeding season and low-temperature environments are likely to limit the body size of bird at high elevations, reflecting montane forest-dependent insectivores with restricted elevational range and low dispersal ability (e.g. understorey babblers and canopy warblers), which also have specific fecundity values imposed by productivity (Ghosh-Harihar, 2014). Gathering further evidence of montane species tracking their optimal or adaptive climatic niches via filtering-related traits is vital for testing the degree of abiotic influence under climate change.

In apparent support of limiting similarity, competition-related traits are those associated with resource-partitioning that potentially contribute to coexistence (Lopez et al., 2016). In phylogenetically dispersed lowland assemblages, we found that trait spacing was generally more even for bill length, vertical stratum and flocking propensity, which are traits related to foraging behaviour, microhabitat selection and resource acquisition (Table 2). For instance bill length and exposed culmen are directly related to a trophic position and feeding strategy, which should be influenced by biotic interactions (Schoener, 1965). In stressful high elevations, efficient use of resources could lead to relatively closely matched culmen-corolla lengths, and thus may lead to the even dispersion of bill size. A similar clustered pattern has been documented for culmen length in hummingbirds (Graham et al., 2012) and leaf warblers (Ghosh-Harihar, 2014). Meanwhile, vertical stratum-use is often related to foraging microhabitat, and may be a source of niche segregation in forest birds (e.g. MacArthur, 1958). Altitude also significantly affected flocking propensity, which showed more even spacing at low elevation. It was noted that positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide (Sridhar et al., 2012). Our previous study indicated that flocking species are susceptible to forest degradation and extreme climate disturbance (Zhang, Han, Huang, & Zou, 2013; Zhang et al., 2016). In this study, CCA ordination showed that most forest flocking specialists, especially understorey insectivore guild were restricted to high elevations (Figure 3b; Figure S7 in Appendix S1). In addition, some specific foraging guilds, such as canopy and mid-storey facultative species (e.g. leaf warblers, shrike babblers) frequently participated in flocks led by a nuclear species, Huet’s Fulvetta Alcippe hueti. Those facultative species also bred above 1,000 m ASL in the Nanling Mountains (Q. Zhang, unpublished data). More data are needed to examine the hypothesized benefits of social flocking along climatic stress gradients, including increasing foraging efficiency and anti-predator vigilance. Such data would help us test whether environmental stress and biotic interactions constrain flocking species establishment through selection on their functional traits.

### 5 | CONCLUSION

Our results identified a novel pattern of increasing bird species richness accompanied by significant decreases in functional diversity along an elevational gradient. Non-random patterns in trait-based metrics revealed that: (a) community assembly was driven primarily by strong environmental filtering which led to increases in evolutionary relatedness and trait convergence in high-elevation sites. Contrarily, species were more dissimilar in lowlands either due to high niche opportunities (high tree diversity) likely permitting coexistence or (directly or indirectly by) competitive exclusion. (b) specific traits were associated with distinct aspects of species’ niches. Filtering-related traits provide environmental tolerance and distinct fecundity values that yield high fitness at high elevations, whereas competitive traits related to behavioural strategies, microhabitat selection and resource acquisition at low elevations. (c) FPD metrics were related to both NDVI and large trees, which can contribute to multi-level filtering in determining the functional composition of bird assemblages. In conclusion, uniform or contrasting patterns of species richness and functional diversity across elevational assemblages highlight that environmental filtering is a predictable and fundamental process of community assembly. Inferences about ecological assembly processes are clearer through an identification of the dispersion of major
functional traits and their relationships to environmental factors, than only through the use of multivariate indices or phylogeny. Understanding such trait-based processes can potentially contribute to ecological differences and ecosystem function for narrowly distributed montane species, particularly under the pressures of global climate change and deforestation.

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DATA AVAILABILITY STATEMENT

The data sets supporting this article are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.z34tmpg7x) (Zhang et al., 2019).

ORCID

Qiang Zhang https://orcid.org/0000-0001-9440-2796
Chuanwu Chen https://orcid.org/0000-0002-3974-853X

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BIOSKETCH

Qiang Zhang is an associate fellow at the Guangdong Institute of Applied Biological Resources, Guangzhou, China. The primary focus of his research is to understand the determinants of multiple facet of biodiversity pattern and social organization (i.e. mixed-species bird flocks) of montane bird assemblages in southern China.

Author contributions: QZ, MH and FSZ conceived the study. QZ, CWC, ZFL, JYL, XLC, AQD and CTY collected, and analysed the data. QZ and MH led the writing of the manuscript and all authors contributed to discussing the results and editing the manuscript.

SUPPORTING INFORMATION

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