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RESEARCH ARTICLE

Temperature and Precipitation Niche Dynamics Shape Avian Elevational Shift Strategies in the Hengduan Mountains

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ABSTRACT

Aim: Intensifying climatic seasonality drives spatial reorganisation in mountains, but the niche processes underlying seasonal elevational shifts remain insufficiently understood. We test how seasonal changes in climate niche position (optima) and niche breadth (the range of climatic conditions that a species experiences over space and time) along temperature and precipitation gradients predict the direction and distance of bird elevational shifts.

Location: Hengduan Mountains, southwest China.

Taxon: Breeding birds.

Methods: We analysed 42,458 records of 206 species from field surveys and citizen-science data. We quantified elevational shift direction and distance using the signed and absolute differences between seasonal median elevations. Using fine-resolution climatic data, we estimated key climatic niche metrics—seasonal optima, annual breadth, seasonal breadth change, and overlap—and evaluated their power to predict shift direction and distance alongside functional traits using phylogenetic Bayesian models.

Results: We identified three post-breeding elevational strategies: upslope, downslope, and resident. Although moving in opposite directions, upslope and downslope shifters exhibited congruent seasonal directions of climatic niche change. Bayesian analyses revealed that shift direction in downslope species was associated with seasonal changes in both climatic optima and niche breadth, whereas for upslope species, it was linked primarily to seasonal niche breadth change. Furthermore, shift distance across both groups corresponded to the magnitude of seasonal niche breadth change, while diet and dispersal capacity showed distinct associations with these spatial responses.

Conclusions: We show that opposing spatial trajectories arise from distinct niche mechanisms. Downslope shifts combine the tracking of climatic optima with seasonal changes in niche breadth, whereas upslope shifts are linked predominantly to the reorganisation of niche breadth. This divergence reflects different sensitivities to mean climatic conditions versus seasonal variability along both temperature and precipitation axes, highlighting that integrating niche position and breadth dynamics is essential for predicting how species redistribute along elevational gradients as seasonal climatic contrasts strengthen.

1 | Introduction

Climate strongly shapes the global distribution of biodiversity (Parmesan et al. 1999; Hällfors et al. 2024). As climatic variability intensifies, shifts in temperature and precipitation alter resource availability, modify habitat suitability, and drive species to reorganise their spatial distributions (Hernández-Carrasco et al. 2025). These redistribution processes are particularly pronounced in mountain ecosystems, where steep environmental gradients compress habitats and amplify the biological consequences of even minor climatic fluctuations (Körner et al. 2017). Mountains therefore provide natural laboratories for understanding how species respond to changing seasonality and for predicting biodiversity dynamics under increasingly variable climates.

Among montane birds, seasonal elevational movements are widespread but directionally diverse (Barçante et al. 2017). Some species descend to lower elevations during the nonbreeding season, while others move upslope into cooler environments (Boyle 2017; Tsai et al. 2021). These contrasting patterns have been attributed to multiple, non-exclusive mechanisms. The climatic constraint hypothesis emphasises temperature avoidance and thermoregulatory limits (Boyle 2011), whereas biotic processes, such as shifts in food availability, nest predation risk, territorial behaviour, and differences in dispersal ability, may also influence movement strategies (Boyle 2008; Barçante et al. 2017; Sheard et al. 2020). In addition to direction, species vary markedly in the distance of their seasonal shifts. Although correlates of movement distance have been explored (Menon et al. 2023), the mechanisms linking the direction of seasonal movements to the distances moved remain poorly resolved. The lack of a unified framework that integrates both direction and distance limits our ability to predict how montane assemblages will reorganise under intensifying climatic seasonality.

The direction and distance of elevational shifts reflect how species reorganise their distributions to cope with seasonally constrained realised niches (John and Post 2022; Neate-Clegg and Tingley 2023). Previous studies typically classified such responses into two general strategies: niche tracking, where species maintain similar climatic conditions across seasons, and niche switching, where they occupy contrasting seasonal environments (Gómez et al. 2016; Zurell et al. 2018). However, the realised niche is multidimensional and can respond to seasonal variation through distinct components (Lu et al. 2021; Cohen and Jetz 2023). Two fundamental aspects are the niche position, representing a species' climatic optimum, and the niche breadth, representing the range of climatic conditions a species occupies within its realised distribution (Lu et al. 2021; Ramón-Martínez and Seoane 2024). Critically, species may exhibit divergent responses in these two components depending on their sensitivity to seasonal climate variability. For instance, some species may shift their niche position while maintaining a constant breadth, whereas others may undergo simultaneous shifts in both components to cope with seasonality (Albright et al. 2010; Cohen and Jetz 2023). Distinguishing how these two components vary seasonally is therefore essential to clarify why species differ not only in the direction but also in the magnitude of their elevational movements.

Regarding the direction of movement, previous interpretations of elevational movements have focused on thermal tolerance limits, such as minimum temperature thresholds (Boyle 2017; Tsai et al. 2021). This limit-based framework successfully explains post-breeding downslope movements driven by winter cold stress but cannot account for the frequent observation of upslope shifts into colder environments (Tsai et al. 2021). Such seemingly counterintuitive movements suggest that elevational responses are not purely passive retreats from physiological boundaries but may also involve the active tracking of climatic niche position. For example, empirical evidence shows that a species' centre of abundance (the spatial expression of its climatic optimum) can shift significantly along environmental gradients even when range boundaries remain stable (Lenoir et al. 2008; Martins, Anderson, et al. 2024). This displacement indicates that species may actively track changing climate optima rather than merely avoiding extremes. Therefore, quantifying seasonal changes in climatic niche optima offers a more mechanistic understanding of the diverse directions of elevational movements.

Complementing niche position, seasonal changes in niche breadth are expected to be particularly important for determining the distance of elevational movements. Species with broader thermal tolerances or greater overlap between their seasonal climatic niches often move shorter distances, as they can persist locally through wider climatic fluctuations (Zurell et al. 2018; Menon et al. 2023). However, most existing models treat niche breadth as a static trait, ignoring that it can vary dynamically across life-history stages (Carscadden et al. 2020; Zurell et al. 2024). For example, climatic constraints during vulnerable periods such as winter often determine realised distributional limits (Carscadden et al. 2020). Consequently, a species with a broad year-round niche may still exhibit a narrow winter niche, necessitating a longer elevational shift to locate specific suitable conditions. Therefore, accurately predicting the distance of these movements requires simultaneous quantification of seasonal changes in niche breadth alongside position.

Understanding niche dynamics in montane environments further requires accounting for multiple climatic dimensions beyond temperature. While temperature has traditionally been considered the dominant driver, recent studies show that precipitation regimes also play a critical role by shaping resource productivity and phenological timing (McCain and Colwell 2011). Sensitivity to these climatic axes often varies along the elevational gradient: high-elevation species tend to be limited by thermal physiology, whereas low-elevation species respond more strongly to precipitation-driven resource fluctuations (Tingley et al. 2009). These climatic sensitivities are further modulated by species' functional traits. For example, dietary specialists such as frugivores or nectarivores are tightly linked to rainfall-driven plant phenology (Boyle 2010), and dispersal capacity determines the extent to which species can physically track shifting climatic optima (Sheard et al. 2020). Integrating these multiple axes of climate with functional ecology is thus crucial for predicting how mountain bird assemblages reorganise under increasing seasonality.

In this study, we combined occurrence records, high-resolution temperature and precipitation data, and functional traits to quantify seasonal changes in niche components (position and breadth), test how these dynamics predict elevational-shift direction and distance, and examine the role of functional traits. Specifically, we asked: (1) How do seasonal changes in climatic niche position and breadth differ between upslope and downslope shift patterns? (2) How do seasonal changes in niche position and breadth predict the direction and distance of elevational shifts across different shift patterns? (3) How are functional traits associated with these spatial responses? By linking climatic niche dynamics and functional traits with elevational shifts, this study elucidates the ecological pathways through which intensifying seasonality reshapes species' spatial distributions in mountain ecosystems.

2 | Methods

2.1 | Study Region

The Hengduan Mountains, located on the southeastern edge of the Tibetan Plateau, support diverse biomes ranging from tropical forests to alpine tundra (Tang 1996). The region exhibits strong vertical gradients in temperature and precipitation, making it an ideal system for testing how seasonal climatic conditions influence elevational shift patterns in montane birds (Figure 1).

2.2 | Data Collection and Cleaning

We delineated the mountainous regions of the study area using the Global Mountain Atlas (v1.2) and compiled bird distribution data collected from 2007 to 2023 (Figure 1). Bird records were obtained from structured line-transect surveys, bird banding, and multiple public observation platforms, including eBird (Cornell Lab of Ornithology 2023), the Global Biodiversity Information Facility (GBIF; GBIF.org 2024a, 2024b, 2024c), and the China Bird Report. To ensure data quality and comparability across heterogeneous sources, all datasets were compiled and processed under a unified standardisation protocol (Johnston et al. 2021; Tsai et al. 2021; Menon et al. 2023). Following integration, all records were standardised as species-level occurrence records for the purpose of estimating seasonal elevational distributions. We retained only verified observations with complete spatiotemporal and effort metadata, treating each distinct transect survey, bird banding event, or complete checklist as an independent sampling event, such that each occurrence record represents the presence of a species within a sampling event. Identical spatial and temporal filters were applied across datasets, and effort filters were harmonised using equivalent criteria where metadata were available (Appendix S1). Spatial filtering was applied based on the latitudinal and longitudinal boundaries of the study area, and records were assigned to either the breeding season (summer; May–August) or non-breeding season (winter; December–February).

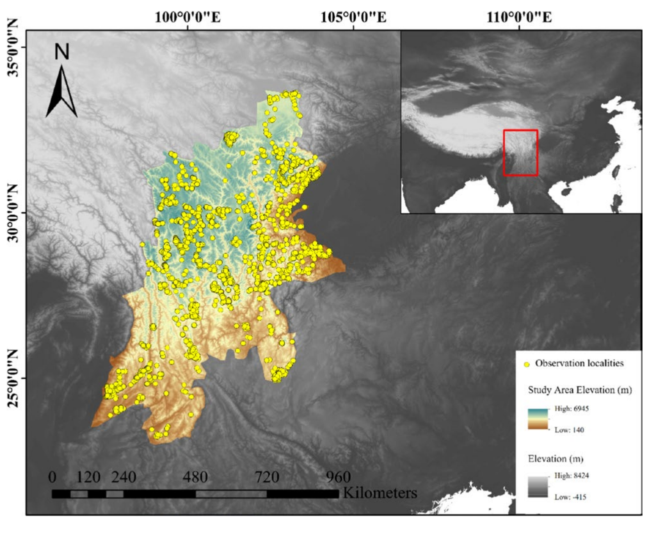

FIGURE 1 | Map of the Hengduan Mountains showing the study area and the spatial distribution of sampling points used to quantify seasonal elevational shifts.

To further enhance data reliability, we excluded occurrence records associated with travel distances exceeding 3 km, observation durations longer than 120 min, or observer groups larger than 10 people. To ensure our analysis focused on local seasonal redistribution, we restricted the dataset to terrestrial species known to breed within the study area and excluded those undertaking long-distance latitudinal migrations following the Handbook of Bird Observations in China (Lu et al. 2021). Furthermore, raptors (Falconiformes and Falconidae) and swifts (Apodidae) were omitted because their high-altitude, high-speed flight behavior can bias elevation estimates. After applying all filtering and quality-control steps, the final dataset comprised 42,458 valid occurrence records representing 206 species (Tables S3 and S4).

2.3 | Calculation of Seasonal Elevation Distribution

To mitigate bias arising from uneven sampling effort across elevation gradients and seasons, we applied a stratified resampling protocol based on occurrence records (Tsai et al. 2021; Menon et al. 2023). To ensure consistency across data sources, elevation values for all occurrence records were extracted from a single 30-arc-second digital elevation model (WorldClim; Fick and Hijmans 2017), replacing elevations reported in the original databases that may vary in accuracy. The study area was divided into eight 500-m altitudinal intervals, with all elevations above 3500 m pooled into a single class due to lower sampling density (Table S1).

Occurrence records were resampled with replacement to equalise sampling effort across each combination of elevation band and season. This procedure was conducted at three sampling intensities corresponding to the first, second, and third quartiles of the distribution of occurrence counts across all elevation-by-season strata. For each intensity level, resampling was repeated 1000 times. In each iteration, we calculated the median (50th percentile), upper boundary (cold boundary; 95th percentile), and lower boundary (warm boundary; 5th percentile) of each species' elevational distribution. To ensure robustness, we retained only species with at least 30 occurrences across all elevational bands in each season (breeding and non-breeding). We also repeated the analysis using a stricter threshold of 60 occurrences per season. Seasonal elevational shifts were quantified as the difference between breeding and non-breeding elevations (breeding minus non-breeding) for each percentile. For each species, 95% confidence intervals (CIs) for these differences were derived from the 1000 resamples. Species were classified as post-breeding downslope shifters if the entire 95% CI was greater than zero, and as upslope shifters if the entire 95% CI was less than zero; species whose 95% CI overlapped zero were classified as showing no clear seasonal elevational shift.

2.4 | Climatic Data and Niche Metrics

To quantify species-specific climatic niches across seasons, we first assembled environmental data within each species' elevational range in the study area. Species' geographic ranges were obtained from BirdLife International and Handbook of the Birds of the World 2021 and clipped to the study area prior to climatic extraction. Climatic variables were extracted from the WorldClim database at 30-arc-second (~1 km) resolution (Fick and Hijmans 2017), including mean temperature (tavg, °C) and mean precipitation (prec, mm). To characterise the fine-scale climatic gradient experienced by each species, we summarised WorldClim mean temperature and precipitation in 100-m elevational bands spanning its geographic range. For each band, we calculated the average climatic conditions across all grid cells occupied by the species, yielding an elevational profile of the climate available within its realised range.

We then derived realised climatic niche (hereafter, "climatic niche") metrics describing seasonal niche position, niche breadth, and niche overlap. Niche position was quantified as the climatic optimum, defined as the combination of temperature and precipitation at which the GAM-predicted occurrence probability was maximal in two-dimensional climate space. For each species and season, we fitted a generalised additive model (GAM) relating occurrence to temperature and precipitation, using background points weighted by a spatial and elevational bias surface. We performed 200 bootstrap iterations and identified the joint maximum of the predicted response surface to obtain seasonal temperature optima (Opt_T) and precipitation optima (Opt_P) (Martins, Anderson, et al. 2024). Seasonal changes in niche position (ΔOpt_T, ΔOpt_P) were then calculated as non-breeding minus breeding values, describing the direction and magnitude of shifts in thermal and hydric conditions between seasons (see Appendix S2 for details).

Niche breadth was quantified with three complementary metrics capturing within-season variability, between-season change, and annual amplitude. Seasonal realised niche breadth (SRNB) was defined as the inter-percentile range ($Q_{0.95}$–$Q_{0.05}$) of temperature ($SRNB_T$) or precipitation ($SRNB_P$) extracted from occurrence records within a season. Seasonal realised niche-breadth variation (SRNBV) was defined, at the species level, as non-breeding minus breeding SRNB for temperature and precipitation ($SRNBV_T$, $SRNBV_P$), indicating whether thermal and hydric niches expand or contract between seasons. Annual niche breadth (ANB) was computed as the same inter-percentile range, but based on all records pooled across the year (ANB_T, ANB_P).

Seasonal climatic niche overlap between breeding and non-breeding periods was measured with Schoener's D (Schoener 1968), which ranges from 0 (no overlap) to 1 (complete overlap). Overlap was calculated in temperature-precipitation space by comparing kernel-smoothed occurrence densities for the two seasons in two-dimensional temperature-precipitation space, implemented with the R package ecospat (Broennimann et al. 2025; Appendix S2).

2.5 | Statistical Analyses

We first compared climatic niche dynamics between upslope and downslope shifters. Within each shift group, we tested whether mean seasonal changes in niche position and breadth (ΔOpt_T, ΔOpt_P, $SRNBV_T$, $SRNBV_P$) differed from zero using phylogenetically informed one-sample tests implemented as intercept-only phylogenetic generalised least squares (PGLS) models. Between groups, we compared the magnitude of seasonal niche changes ($|\Delta Opt_T|$, $|\Delta Opt_P|$, $|SRNBV_T|$, $|SRNBV_P|$), seasonal niche overlap (Schoener's D), and annual niche breadth (ANB_T, ANB_P) using PGLS models with shift group as a predictor. Phylogenetic non-independence among species was modelled using Pagel's λ estimated by maximum likelihood. Model assumptions were evaluated using residual diagnostics.

To select functional traits relevant to elevational-shift patterns for subsequent modelling, we employed a screening procedure. Seven candidate traits were selected a priori based on hypotheses regarding food availability, nest predation risk, territorial behaviour, and dispersal ability (see Appendix S3 for details). These included the hand-wing index as a proxy for dispersal capacity (Sheard et al. 2020), territoriality score (Tobias et al. 2016), clutch type (Wang et al. 2021), and the proportional dependence on four diet types (invertivore, frugivore, granivore, nectarivore) (Wilman et al. 2014). For each of six independent data subsets (differing in resampling intensity and observation thresholds), we fitted univariate phylogenetic generalised least-squares (PGLS) models in which seasonal elevational shifts in the lower, median, or upper range limit were treated as the response variable. PGLS models were fitted using gls() with a Pagel's λ correlation structure implemented via corPagel(). Models were implemented in ape, phangorn, and nlme (Paradis and Schliep 2019; Schliep 2011; Pinheiro et al. 2024). Phylogenetic covariance was derived from a maximum-clade-credibility tree built from 1000 "Hackett All Species" trees (Jetz et al. 2012). We assumed Brownian-motion evolution ($\lambda = 1$) and conducted sensitivity analyses by also estimating λ via maximum likelihood (Appendix S3). Model residuals were inspected using residual-versus-fitted and quantile-quantile plots to confirm approximate normality and homoscedasticity. We applied a consistency filter and retained only traits that showed significant relationships in at least three subsets for inclusion in the final models (Appendix S3).

Finally, we fitted Bayesian phylogenetic mixed models using MCMCglmm (Hadfield 2010) to evaluate how climatic metrics and the selected functional traits predict elevational shifts. Shift direction was defined as the signed difference between breeding and non-breeding median elevations (breeding minus non-breeding; positive values indicate post-breeding downslope shifts) and shift distance as the absolute value of this difference. We constructed specific predictor sets to test the hypotheses. For shift direction, we tested whether movement is driven by niche position tracking or breadth constraints. We fitted two climatic predictor sets: (i) $\Delta Opt_T + \Delta Opt_P + D$, assessing how shifts in climatic optima (tracking) relate to direction while controlling for overall niche conservatism; and (ii) $SRNBV_T + SRNBV_P$, assessing how seasonal expansion/contraction of niche breadth (constraints) relates to direction. For shift distance, we tested whether movement magnitude is shaped by ecological generalism or seasonal restructuring. We fitted three sets: (i) $|SRNBV_T| + |SRNBV_P|$, describing the magnitude of seasonal niche restructuring; (ii) $ANB_T + ANB_P$, describing annual niche breadth (generalism); and (iii) D, describing overall seasonal overlap.

Each selected functional trait was then added individually alongside the climatic predictors to minimise multicollinearity and assess its association with elevational responses after accounting for climatic drivers. Models were fitted separately for upslope and downslope shifters to test for strategy-specific effects. We considered predictor effects to be statistically significant if the 95% credible intervals (CI) of their posterior distributions did not overlap zero. All Bayesian models included phylogeny as a random effect, assumed Gaussian residuals, and used weakly informative priors (inverse-Wishart priors for variance components: $V = 1, \nu = 0.002$; see Appendix S4). For each model, we ran a single MCMC chain for 120,000 iterations (5000 burn-in, thinning 20). Convergence was rigorously assessed using trace plots, effective sample sizes (ESS > 200), and Heidelberger-Welch diagnostics. Key models underlying the main text inferences were additionally validated using independent chains, which converged to the same posterior distributions. All analyses were performed in R 4.4.2 (R Core Team 2024).

3 | Results

3.1 | Elevational Shift Patterns and Seasonal Climatic Niche Dynamics

The final dataset comprised 42,458 occurrence records for 206 species. Most records came from structured field surveys (line transects and bird banding; 55.6%), followed by the China Bird Report and eBird (41.2%), with a smaller contribution from GBIF (3.2%; Appendix S1, Tables S3 and S4).

Across species, three elevational shift types emerged. Upslope shifters (breeding at lower elevations and occurring at higher elevations in the non-breeding season) accounted for 18%–19% of species ($n = 18$, 33, and 39 under low, medium, and high resampling intensity, respectively). Downslope shifters comprised 46%–51% ($n = 47$, 83, and 96), and the remaining 29%–34% showed no detectable seasonal elevational shift ($n = 27$, 55, and 71). Mean elevational midpoints further highlighted these contrasts. Upslope shifters ascended from 1462 ± 3.63 m in the breeding season to 1871 ± 3.93 m in the non-breeding season (Figure 2a), whereas downslope shifters decreased from 2603 ± 3.06 m to 2026 ± 3.11 m. Species with no significant seasonal shift occupied intermediate elevations (1770 ± 3.43 m to 1932 ± 3.92 m).

Seasonal climatic niche dynamics differed between upslope and downslope shifters overall (Figure 2). Despite contrasting movement directions, both groups showed comparable seasonal niche overlap (Figure 2b). For both groups, seasonal niche optima shifted toward cooler and drier conditions in the non-breeding season relative to the breeding season (Figure 2c). Seasonal changes in niche breadth were also evident but differed between groups. Temperature niche breadth decreased in the non-breeding season among downslope shifters but increased among upslope shifters, whereas precipitation niche breadth expanded in the non-breeding season in both groups (Figure 2d). However, the magnitude of these seasonal changes in niche components differed significantly between groups. Upslope shifters showed stronger seasonal variation in precipitation optima, whereas seasonal variation in temperature optima did not differ between groups (Figure 2e). In contrast, downslope shifters exhibited greater seasonal variation in climatic niche breadth along both temperature and precipitation axes and also possessed broader annual climatic niche breadths (Figure 2f,g). These seasonal and between-group patterns in climatic optima, overlap, and niche breadth were qualitatively consistent across the five alternative resampling datasets (Tables S5 and S6).

3.2 | Climatic Correlates of Elevational-Shift Direction and Distance

Climatic niche components were significantly associated with both the direction and distance of elevational shifts (Figure 3). In the downslope models, both niche position and niche breadth metrics were associated with shift direction (Figure 3a). For niche position, species tracking warmer climatic optima tended to move downslope across upper, median, and lower boundaries, while those tracking wetter climatic optima tended to move downslope at median and lower boundaries. For niche breadth, however, temperature and precipitation showed contrasting effects. Broader winter temperature niche breadth was associated with a reduced tendency to move downslope at upper and median boundaries. In contrast, broader winter precipitation niche breadth was associated with an enhanced tendency to move downslope at median and lower boundaries. In upslope models, climatic drivers were less numerous; only an expanded winter temperature niche breadth was associated with an increased tendency for upslope shifts, particularly at median and lower boundaries, with no other significant climatic predictors.

Shift distance was mainly related to annual niche breadth and the magnitude of seasonal niche breadth change (Figure 3b). In downslope models, larger annual temperature ranges consistently predicted greater shift distances across all boundaries. In addition, larger seasonal change in temperature niche breadth was associated with greater shift distance at upper boundaries, whereas larger seasonal change in precipitation niche breadth was associated with greater shift distance at lower boundaries. In upslope models, relationships were more restricted; only greater seasonal change in precipitation niche breadth was associated with increased shift distances, specifically near median elevations.

These patterns were robust across sensitivity analyses. Results from the five alternative resampled datasets remained qualitatively consistent with the main dataset, maintaining the same directionality of climatic effects on both shift direction and distance, although the statistical strength of these associations varied slightly among datasets (Tables S7 and S8).

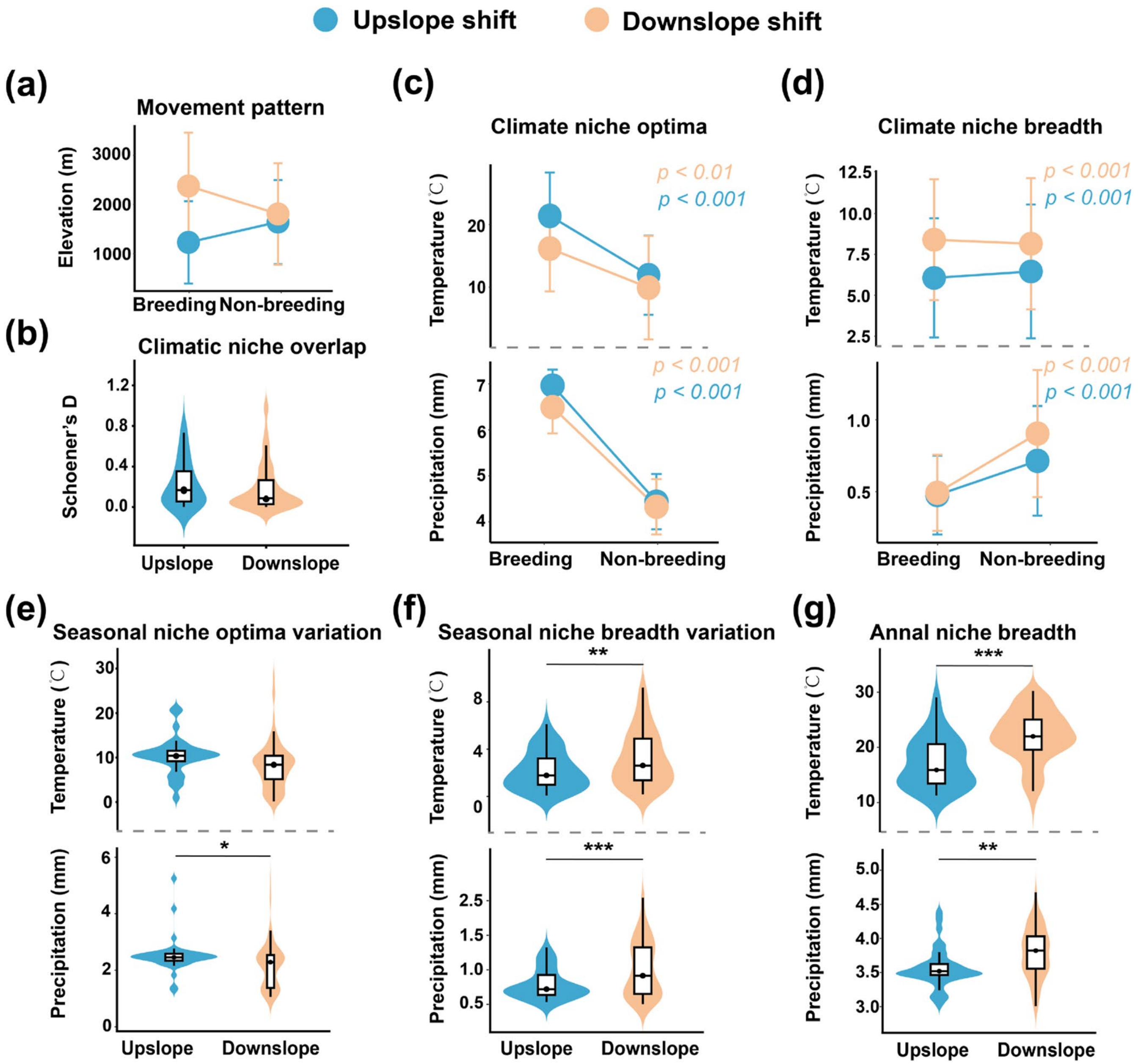

FIGURE 2 | Seasonal elevational shifts and climatic niche dynamics for upslope and downslope shift patterns. (a) Seasonal shifts in elevational midpoints for upslope and downslope shifters. (b) Comparison of seasonal climatic niche overlap (Schoener's D) between upslope and downslope shifters. (c) Seasonal changes in temperature and precipitation optima within each shift group. (d) Seasonal changes in temperature and precipitation niche breadth within each shift group. (e) Differences between upslope and downslope shifters in the seasonal change of temperature and precipitation optima. (f) Differences between upslope and downslope shifters in the seasonal change of temperature and precipitation niche breadth. (g) Differences in annual temperature and precipitation niche breadth between upslope and downslope shifters. For (c) and (d), *p*-values from phylogenetically informed within-group tests are displayed in the upper-right corner of each panel. For (e–g), asterisks indicate significant between-group differences based on phylogenetically informed analyses (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$); "ns" denotes non-significance. Results shown are based on the highest-intensity resampling dataset for species with ≥ 30 valid seasonal occurrence records. Full statistical results across all resampling scenarios and observation thresholds are provided in Tables S5 and S6.

3.3 | Trait Correlates of Elevational-Shift Direction and Distance

Trait-based model results indicated that effects on elevational shifts varied distinctly between downslope and upslope patterns, with diet composition acting as the primary driver for downslope shifters while both dispersal ability and diet influenced upslope shifters (Table Sa; Figure 4). For shift direction among downslope shifters, diet composition showed the most consistent relationships. Species with a higher proportion of invertebrates in their diet exhibited a greater tendency to move downslope, particularly at upper and median boundaries. Conversely, species with a seed-based diet showed a reduced tendency to move downslope at lower and median boundaries, although statistical significance varied among models. In upslope models, dispersal ability played a key role, where species

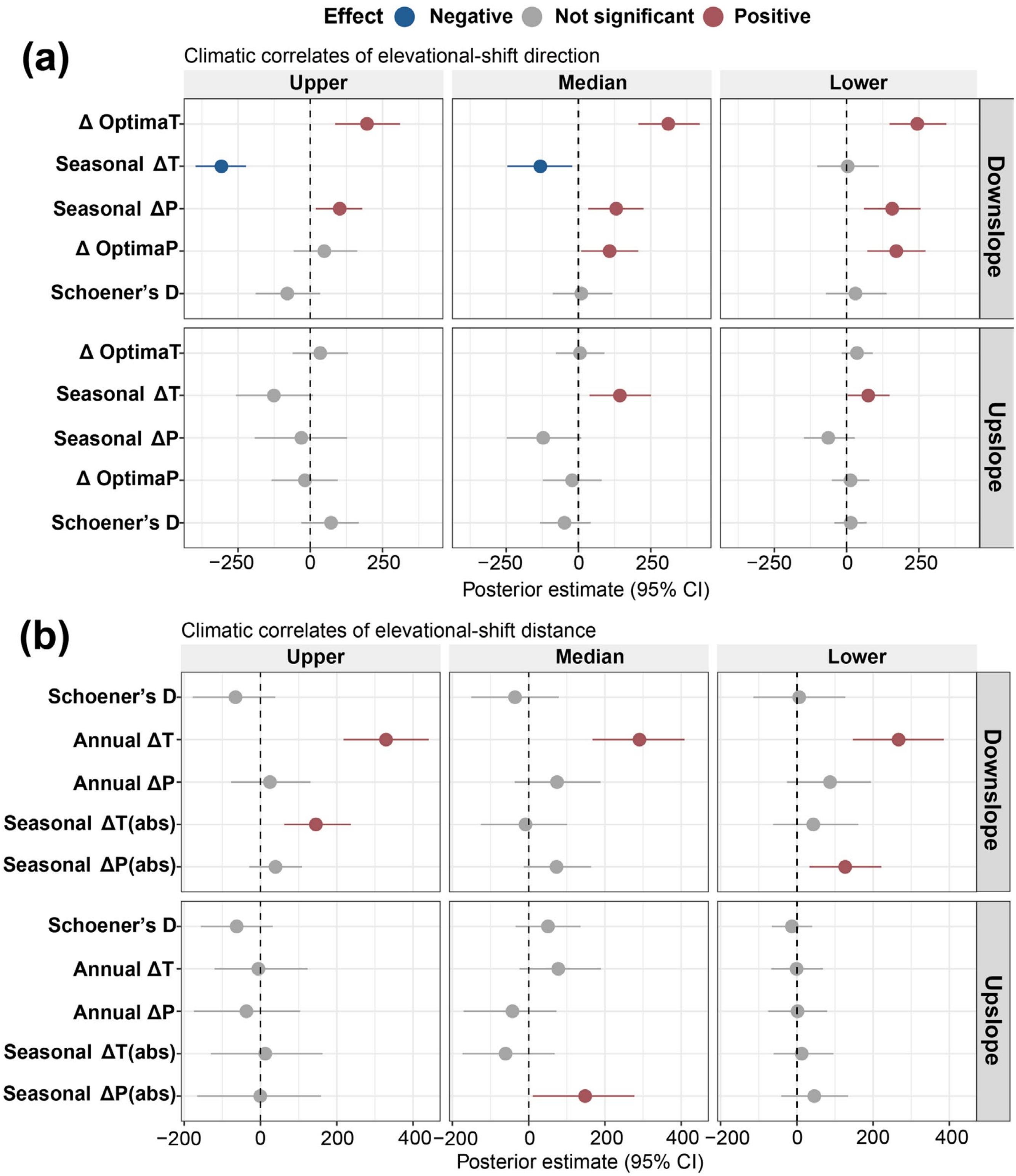

FIGURE 3 | Bayesian phylogenetic model estimates of climatic associations with elevational-shift direction and distance. (a) Model estimates for elevational-shift direction. (b) Model estimates for elevational-shift distance. For shift-direction models, positive effect estimates indicate a stronger tendency toward the modelled shift direction (upslope or downslope), as defined within each group-specific model. For shift-distance models, effect estimates reflect changes in the absolute magnitude of elevational shifts, with positive values indicating increased shift distance. ΔT = temperature range, ΔP = precipitation range, abs = absolute difference. Points and bars represent posterior means ±95% credible intervals from MCMCglmm models fitted for species with at least 30 valid occurrence records, summarised at the highest resampling intensity. Colours indicate the direction and statistical significance of the modelled effects. Full results for additional resampling intensities and higher observation thresholds are provided in Tables S7 and S8.

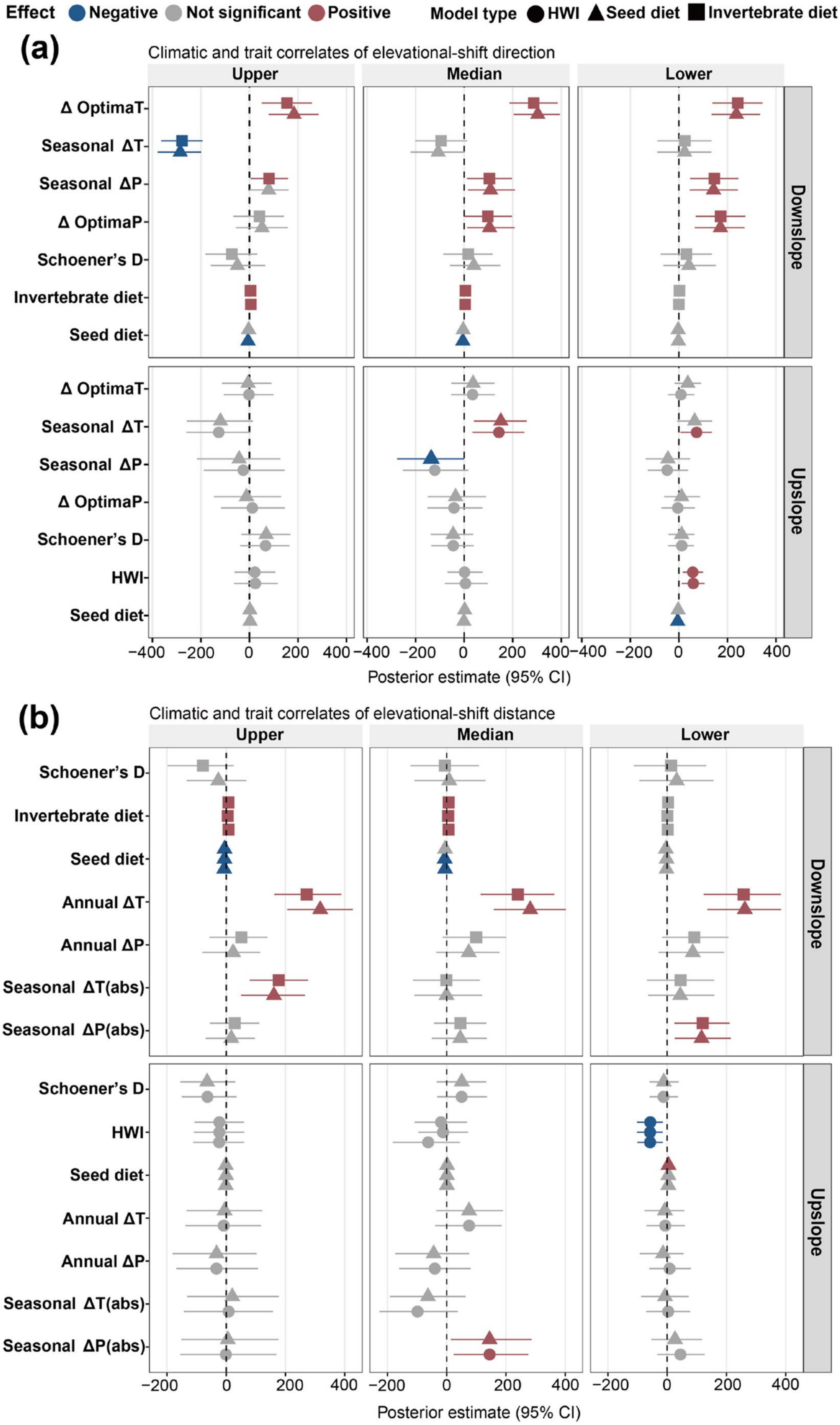

FIGURE 4 | Legend on next page.

FIGURE 4 | Bayesian phylogenetic model estimates of combined climatic and trait associations with elevational-shift direction and distance. (a) Model estimates for elevational-shift direction. (b) Model estimates for elevational-shift distance. For shift-direction models, positive effect estimates indicate a stronger tendency toward the modelled shift direction (upslope or downslope), as defined within each group-specific model. For shift-distance models, effect estimates reflect changes in the absolute magnitude of elevational shifts, with positive values indicating increased shift distance. ΔT = temperature range, ΔP = precipitation range, abs = absolute difference. Points and bars represent posterior means ±95% credible intervals from MCMCglmm models fitted for species with at least 30 valid occurrence records, summarised at the highest resampling intensity. Colours indicate the direction and significance of estimated effects, and each shape denotes a different trait-specific model. Full results for other sampling thresholds and resampling levels are available in Tables S9 and S10.

with a higher hand-wing index (HWI) showed stronger upslope tendencies at lower boundaries. Similar to downslope patterns, seed-based diets were associated with weaker tendencies for upslope movement, though this effect also showed variable significance across models.

For shift distance, downslope shifters with a higher proportion of invertebrates moved longer distances at upper and median boundaries, whereas species with seed-based diets moved shorter distances. Among upslope shifters, dispersal constraints were evident as species with a higher HWI were associated with shorter shift distances, particularly at lower boundaries. Sensitivity analyses across alternative resampling datasets yielded qualitatively similar trait patterns for downslope shifters, whereas trait associations for upslope shifters were less consistent in both direction and statistical support (Tables S9 and S10).

4 | Discussion

4.1 | Convergent Climatic Optima Achieved Through Divergent Niche Reorganisation Strategies

Our results indicate that upslope and downslope shifters exhibit congruent seasonal directions of climatic niche optima change. Specifically, both groups track warmer and wetter conditions during the breeding season and cooler and drier conditions during the non-breeding season. This consistency implies a shared physiological requirement to synchronise with favourable temperature-moisture regimes and the timing of resource availability (Tellería and Pérez-Tris 2003; Zurell et al. 2018). Crucially, this convergence helps resolve the apparent paradox of winter upslope shifts. Rather than moving into intrinsically harsher environments, upslope shifters reach the functionally similar cool, dry seasonal optima as downslope shifters by moving into different parts of the elevational gradient. Consequently, upslope and downslope shifts function not as opposing behaviours but as equivalent responses to seasonal climatic forcing. Such spatial redistribution enables both groups to remain aligned with favourable abiotic conditions throughout the annual cycle.

Although they share this seasonal climatic target, the two groups employ divergent mechanisms to reorganise their niches. Upslope shifters primarily adjust climatic niche position, with a stronger seasonal shift in hydric optima, consistent with the idea that seasonal redistribution can track specific axes of climatic space rather than temperature alone (Tingley et al. 2009). Downslope shifters, by contrast, display marked reorganisation of climatic niche breadth across both climatic axes. The thermal breadth contracts from the breeding to the non-breeding season, whereas hydric breadth expands, indicating axis-specific constraints and flexibility across the annual cycle. This seasonal asymmetry is consistent with the view that climatic constraints can be season- and component-dependent, and that population persistence may be shaped by the most constrained period of the annual cycle (Carscadden et al. 2020).

4.2 | Distinct Niche Components Shape the Direction and Distance of Seasonal Elevational Redistribution

We found that the direction and the distance of seasonal elevational shifts are shaped by partly distinct niche processes, and that the relative importance of these processes differs between downslope and upslope shifters. This supports the hypothesis that species respond to seasonal environments either by tracking shifts in the position of their realised climatic niche or by reorganising the range of climatic conditions they use (Gómez et al. 2016; Cohen and Jetz 2023). Specifically, movement direction is primarily associated with seasonal shifts in climatic niche position and the direction of change in realised niche breadth, whereas movement distance is governed by the magnitude of seasonal niche restructuring and overall annual niche breadth, with the relative importance of these components differing between downslope and upslope shifters.

For downslope shifters, movement direction depends on a combination of optimal conditions and seasonal constraints. Species showing stronger seasonal shifts in climatic optima between breeding and non-breeding seasons were more likely to exhibit downslope redistribution, consistent with the idea that directional movement reflects seasonal tracking of realised climatic niche position (Lenoir et al. 2008). At the same time, species that show stronger winter-associated narrowing of realised niche breadth exhibit clearer directional shifts, supporting the view that migration occurs when winter conditions restrict the usable climatic range (Boyle 2017). Within these movements, we observed distinct boundary-specific responses where shifts at cold range boundaries are associated with thermal niche breadth, while shifts at warm boundaries align more closely with precipitation optima. These associations match the expectation that cold edges are constrained by low-temperature stress, whereas warm edges are shaped by water availability (Tingley et al. 2012; Ferger et al. 2014). Thus, downslope movements reflect a combined response to shifting climatic optima and boundary-specific limiting factors rather than to thermal extremes alone.

The distance of downslope shifts is further shaped by ecological generalism and the capacity for seasonal niche restructuring. We found that species with broader annual niche breadth tend to move farther along elevational gradients. This finding contrasts with expectations under a physiological-tolerance perspective, in which broad thermal tolerance is often assumed to promote residency by allowing persistence through local fluctuations (Zurell et al. 2018; Menon et al. 2023). The discrepancy likely stems from a distinction between fundamental and realised niche dimensions (Hutchinson 1957; Soberon and Peterson 2005). While physiological tolerance reflects the capacity to endure conditions, realised niche breadth reflects the ecological capacity to exploit diverse resources. Consequently, generalist species appear to leverage this ecological flexibility to access spatially distant habitats rather than to buffer against the need for movement. Likewise, species showing larger absolute seasonal changes in niche breadth also possess greater flexibility to reorganise their climatic associations, facilitating more extensive shifts. These findings align with evidence that species with wider climatic niches tend to undergo larger range shifts under environmental change (Carscadden et al. 2020; Hällfors et al. 2024). Our analysis adds a seasonal dimension to this pattern, demonstrating that annual niche magnitude and seasonal restructuring jointly predict the extent of downslope redistribution.

Patterns in upslope shifters differ fundamentally because their movements appear decoupled from the tracking of climatic optima. Instead, the seasonal restructuring of niche breadth emerges as the sole dominant driver determining their spatial redistribution. Specifically, we found that species exhibiting greater seasonal compression or expansion of their realised niche moved significantly farther upslope. This reliance on breadth dynamics alone suggests that upslope movement is not a pursuit of a shifting thermal target, but rather a capacity-dependent response. This interpretation aligns conceptually with tolerance-based perspectives proposed in previous studies (Janzen 1967; Freeman et al. 2019), suggesting that upslope distributions may be constrained by the capacity to endure harsh, variable conditions rather than by the availability of preferred climates. Consequently, while downslope shifts reflect a target-oriented tracking strategy involving both niche position and breadth, upslope shifts represent a capacity-driven strategy shaped almost exclusively by dynamic niche restructuring. Although climatic niche dynamics emerge as primary drivers, elevational redistribution may also be influenced by habitat structure, microhabitat availability, and biotic interactions that covary with climate along elevational gradients (Ferger et al. 2014; Freeman et al. 2019). Considering these factors alongside climatic niche dynamics may further improve our understanding of elevational redistribution and underscores the value of future research integrating finer-scale ecological and mechanistic data (Neate-Clegg and Tingley 2023).

4.3 | Diet and Dispersal Mediate the Direction and Distance of Elevational Shifts

Species traits influence both the direction and the distance of seasonal elevational shifts through distinct but complementary pathways. For species that move downslope in winter, both the tendency to shift and the distance are linked to dietary composition. Invertebrate-based specialists exhibit stronger downslope responses and move farther along the elevational gradient, whereas seed-based specialists shift less. This pattern is consistent with the foraging-limitation hypothesis, which predicts that elevational shifts are more likely when local food resources decline strongly or unpredictably through the year (Boyle 2011). At high elevations, invertebrate abundance declines during cold periods. In contrast, lower elevations maintain more accessible prey and provide better cover. Thus, insectivorous species tend to follow prey availability downslope (Tsai et al. 2021; Neate-Clegg and Tingley 2023). However, seed-based species show little winter downslope movement at upper boundaries, likely because seed resources are relatively stable seasonally, reducing the need for elevational shift (Boyle 2011). In addition, toward the upper limits of species' ranges, the energetic or physical quality of available seeds may decline. Individuals may partially compensate by selectively exploiting higher-energy or larger seeds, a strategy analogous to resource optimization documented in frugivorous birds (Martins, Stouffer, et al. 2024). This capacity to adjust diet quality allows seed-eating birds to remain in place instead of moving downslope.

Winter upslope shifts show a different pattern, related to dispersal capacity and the stability of seed resources. At lower elevational boundaries, species with higher hand-wing index (HWI) show greater elevational shift distances, consistent with the dispersal-ability hypothesis linking broader movements to higher intrinsic mobility (Sheard et al. 2020; Menon et al. 2023). This capability facilitates a greater tendency for upslope movement during winter, although overall movement distance remains limited. In contrast, seed-based specialists are less likely to initiate upslope shifts, but when such shifts occur, they tend to involve longer distances at lower boundaries. This seemingly counterintuitive pattern likely reflects resource limitation at the lower elevational margin. Seed resources are generally abundant and seasonally stable at low elevations, which reduces the need for regular upslope movement (Boyle 2011). However, when these resources become depleted or competition intensifies, individuals may be forced to shift farther to find suitable foraging areas. Similar processes have been observed in tropical montane systems, where spatial heterogeneity and the seasonal scarcity of plant resources trigger extensive elevational movements in herbivorous birds (Boyle 2011; Haase et al. 2025). These results therefore reinforce the idea that upslope shifts align more closely with ecological opportunity and trait-mediated flexibility than with direct climatic tracking, matching studies that interpret winter upslope shifts as responses to habitat access and release from competition rather than simple responses to macroclimate (Tsai et al. 2021; Freeman et al. 2019; Williamson and Witt 2021).

4.4 | Conservation Implications and Future Perspectives

Understanding the distinct niche mechanisms driving elevational redistribution is critical for identifying conservation priorities in the Hengduan Mountains, a biodiversity hotspot where increasing climatic variability and intensifying human pressure are rapidly reshaping species ranges (Freeman et al. 2018; Yin et al. 2020). Our results reveal clear differences in vulnerability among elevational movement strategies. Species whose seasonal redistribution requires the concurrent tracking of climatic niche position and the reorganisation of niche breadth tend to be more sensitive to climatic perturbations (Cohen and Jetz 2023). In this study, downslope shifters exhibit this form of compounded sensitivity, as their movements depend simultaneously on tracking specific climatic optima and on adjusting niche breadth in response to winter conditions. As a consequence, disruption to either thermal or hydric regimes may impair their ability to maintain effective seasonal connectivity along elevational gradients. In contrast, upslope shifters are influenced primarily by variation in niche breadth and appear to exhibit a different mode of resilience, characterised by greater flexibility in realised niche use and reliance on persistence under variable conditions rather than on directional climatic tracking.

This differential vulnerability underscores the urgent need to maintain spatial connectivity along elevational gradients. Ongoing habitat loss, infrastructure expansion, and grazing are fragmenting mid-elevation forests, thereby disrupting the corridors that sensitive downslope shifters use for seasonal movement (Robinson and Wilcove 1994; La Sorte and Jetz 2010). As landscape changes accumulate, they progressively constrain elevational connectivity and how these species realise their climatic niches, reducing their capacity for necessary elevational adjustments. Conservation planning should therefore prioritise the protection of mid-elevation forests and moisture-retaining refugia to preserve continuous environmental gradients (Krosby et al. 2010; Morelli et al. 2016). Ensuring access to these structurally complex habitats during both breeding and non-breeding seasons is essential to sustain the rigorous tracking requirements of downslope shifters (Boyle 2010; Ferger et al. 2014).

Addressing this evolving elevational landscape will require integrating climate science with active habitat management. Management actions should anticipate changes in resource phenology under continued warming and target interventions where elevational redistribution is most threatened. Protecting cool corridors at cold boundaries and moisture-retaining refugia at warm boundaries enhances the behavioural flexibility that underlies resilience to climatic variability. Finally, such management efforts should be supported by long-term monitoring that integrates remote sensing, acoustic surveys, and in situ tracking, enabling evaluation of how land use and climate together reshape these dynamics, ultimately securing the processes of behavioural niche adjustment that buffer montane bird diversity against environmental change (John and Post 2022; Neate-Clegg and Tingley 2023).

5 | Conclusion

Our findings demonstrate that seasonal elevational shifts are not simple upslope or downslope movements along a single temperature gradient. Instead, they reflect the reorganisation of realised climatic niches along both temperature and precipitation axes through changes in niche position and niche breadth. Upslope and downslope shifters respond to the same seasonal climatic rhythm but rely on different niche components, with downslope species combining shifts in climatic optima with seasonal constraints on niche breadth, whereas upslope species are driven primarily by the restructuring of niche breadth. By linking these niche dynamics to functional traits, our study connects environmental filtering with life-history constraints and helps explain how contrasting elevational strategies can coexist within the same mountain assemblage. This perspective highlights the joint reorganisation of niche position and niche breadth as a key dimension structuring both the direction and the distance of species' elevational responses to climate change. As seasonal climatic contrasts continue to shape mountain environments, understanding how species reorganise their realised climatic niches, rather than simply tracking changes in mean temperature, will be essential for predicting the resilience of montane biodiversity.

Author Contributions

S.Z.: conceptualisation; data curation; formal analysis; methodology; visualisation; writing – original draft; writing – review and editing. Y.C.: data curation. Y.W.: data curation. J.Z.: data curation. J.R.: data curation. M.L.: writing – review and editing. Y.W.: writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.5mkkwh7hh.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Distribution of bird checklists used in the study for each elevational band and season combination. **Table S2:** To test whether geometric constraints result in elevation shifts, we calculated relative elevation shifts by dividing the absolute value of the elevation shift by the breeding-season elevation at each elevation limit (i.e., elevation shift at the upper limit/breeding elevation at the upper limit, and so on). We then tested the association between the relative elevation shift of species across all sampling efforts and the breeding-season elevation of their respective elevational distributions. Shown are the outputs of linear regression models examining the relationship between relative elevation shifts at the lower, middle, and upper elevational limits and breeding-season elevation for different resampling intensities and minimum numbers of observations (30 or 60) in the dataset. "Database" indicates the minimum number of observations (≥ 30 or ≥ 60) and the level of sampling effort: 1 = low, 2 = medium, 3 = high. **Table S3:** Seasonal elevational movement types of species and differences in upper, middle, and lower elevational limits (elevational difference = breeding-season elevation − non-breeding-season elevation) in low-, medium-, and high-effort resampling datasets with ≥ 30 observations. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season. **Table S4:** Seasonal elevational movement types of species and differences in upper, middle, and lower elevational limits (elevational difference = breeding-season elevation − non-breeding-season elevation) in low-, medium-, and high-effort resampling datasets with ≥ 60 observations. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season. **Table S5:** Descriptive statistics and phylogenetically informed comparisons of climatic variables between upslope and downslope migrants under different resampling intensities and minimum observation thresholds (30, 60). ΔT_opt = seasonal change in temperature niche optimum (non-breeding minus breeding); ΔP_opt = seasonal change in precipitation niche optimum (non-breeding minus breeding); SRNBV_T = seasonal variation in realised temperature niche breadth; SRNBV_P = seasonal variation in realised precipitation niche breadth; ANB_P = precipitation annual niche breadth; ANB_T = temperature annual niche breadth; SchoenerD = seasonal overlap in climatic niches. Climatic values are presented as mean ± standard error. "Dataset" indicates the minimum number of observations (≥ 30 or ≥ 60) and the level of sampling effort: 1 = low, 2 = medium, 3 = high. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season. **Table S6:** Descriptive statistics and phylogenetically informed within-group comparisons of climatic niche traits between breeding and non-breeding seasons under different resampling intensities and minimum observation thresholds (30, 60). T_optimum = temperature niche optimum; P_optimum = precipitation niche optimum; SRNB_T = seasonal realised temperature niche breadth; SRNB_P = seasonal realised precipitation niche breadth. Climatic niche trait values are presented as mean ± standard error. "Dataset" indicates the minimum number of observations (≥ 30 or ≥ 60) and the level of sampling effort: 1 = low, 2 = medium, 3 = high. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season. **Table S7:** Bayesian model results estimating the effects of the direction of elevational shift patterns, based on varying resampling efforts and minimum observation counts (≥ 30 or ≥ 60). ΔT_opt = seasonal change in temperature niche optimum (non-breeding minus breeding); ΔP_opt = seasonal change in precipitation niche optimum (non-breeding minus breeding); SRNBV_T = seasonal variation in realised temperature niche breadth; SRNBV_P = seasonal variation in realised precipitation niche breadth. "Dataset" indicates the minimum number of observations (≥ 30 or ≥ 60) and the level of sampling effort: 1 = low, 2 = medium, 3 = high. Results are categorised into three types: median_diff = centre, upper_diff = upper boundary, and lower_diff = lower boundary, corresponding to different parts of the elevational distribution. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season. **Table S8:** Bayesian model results estimating the effects of the magnitude of elevational shift patterns, based on varying resampling efforts and minimum observation counts (≥ 30 or ≥ 60). SRNBV_Tabs = absolute magnitude of seasonal variation in realised temperature niche breadth; SRNBV_Pabs = absolute magnitude of seasonal variation in realised precipitation niche breadth; ANB_P = precipitation annual niche breadth; ANB_T = temperature annual niche breadth; SchoenerD = seasonal overlap in climatic niches. "Dataset" indicates the minimum number of observations (≥ 30 or ≥ 60) and the level of sampling effort: 1 = low, 2 = medium, 3 = high. Results are categorised into three types: median_diff = centre, upper_diff = upper boundary, and lower_diff = lower boundary, corresponding to different parts of the elevational distribution. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season. **Table S9:** Bayesian model results estimating the effects of the direction of elevational shift patterns together with species traits, based on varying resampling efforts and minimum observation counts (≥ 30 or ≥ 60). ΔT_opt = seasonal change in temperature niche optimum (non-breeding minus breeding); ΔP_opt = seasonal change in precipitation niche optimum (non-breeding minus breeding); SRNBV_T = seasonal variation in realised temperature niche breadth; SRNBV_P = seasonal variation in realised precipitation niche breadth; Seed diet = proportion of seeds in the diet; HWI = hand-wing index; Invertebrate diet = proportion of invertebrates in the diet. "Dataset" indicates the minimum number of observations (≥ 30 or ≥ 60) and the level of sampling effort: 1 = low, 2 = medium, 3 = high. Results are categorised into three types: median_diff = centre, upper_diff = upper boundary, and lower_diff = lower boundary, corresponding to different parts of the elevational distribution. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season. **Table S10:** Bayesian model results estimating the effects of the magnitude of elevational shift patterns together with species traits, based on varying resampling efforts and minimum observation counts (≥ 30 or ≥ 60). SRNBV_Tabs = absolute magnitude of seasonal variation in realised temperature niche breadth; SRNBV_Pabs = absolute magnitude of seasonal variation in realised precipitation niche breadth; ANB_P = precipitation annual niche breadth; ANB_T = temperature annual niche breadth; SchoenerD = seasonal overlap in climatic niches; Seed diet = proportion of seeds in the diet; HWI = hand-wing index; Invertebrate diet = proportion of invertebrates in the diet. "Dataset" indicates the minimum number of observations (≥ 30 or ≥ 60) and the level of sampling effort: 1 = low, 2 = medium, 3 = high. Results are categorised into three types: median_diff = centre, upper_diff = upper boundary, and lower_diff = lower boundary, corresponding to different parts of the elevational distribution. "Upslope shift" indicates species that breed at lower elevations and move to higher elevations in the non-breeding season; "downslope shift" indicates species that breed at higher elevations and move to lower elevations in the non-breeding season.