

Himalayan birds that show the greatest elevational shifts remain within the narrowest thermal regimes

Tarun Menon¹  | Vijay Ramesh²  | Sahas Barve^{3,4}

¹Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India

²K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, New York, USA

³Division of Birds, Smithsonian National Museum of Natural History, Washington, District of Columbia, USA

⁴Avian Ecology Program, Archbold Biological Station, Florida, Venus, USA

Correspondence

Tarun Menon, Centre for Ecological Sciences, Indian Institute of Science, Bengaluru 560012, India.
Email: tarunmenon15@gmail.com

Handling Editor: Catherine Sheard

Abstract

Aim: Elevational migration is a globally ubiquitous animal behaviour. Understanding the mechanisms that drive variation in elevational movement can help explain the evolution of this widespread animal behaviour and its role in shaping montane life history. We examine the role of thermal regime (the intra-annual variation in temperature experienced by a species), dispersal ability and diet in explaining the extent of elevational movements.

Location: Eastern and Western Himalayas.

Time Period: 2011–2022.

Major Taxa Studied: Birds.

Methods: We used community science data from eBird to acquire checklist-based observations of birds and used comprehensive data cleaning procedures and randomization tests to produce estimates of seasonal elevational shifts for 302 species of Himalayan birds. Using these data, we ran phylogenetic least squares regressions (PGLS) to test if the extent of elevational shift is driven by thermal regime, dispersal ability and diet.

Results: Most Himalayan birds (up to 65%) showed downslope shifts in the winter, although some (5%–10%) low elevation species shifted upslope. Elevational shift was negatively associated with a species' thermal regime. Species that showed the greatest elevational shifts in both eastern and western Himalayas moved within the narrowest intra-annual temperature regimes, but did not match their breeding range temperatures as closely as possible. Diet influenced elevational shift in both eastern and western Himalayas, while dispersal ability did not drive elevational shifts.

Main Conclusions: Species that show the biggest elevational shifts track thermal regimes most closely. However, in addition to tracking thermal regimes, diet and potentially habitat availability/preferences may drive seasonal elevational shifts. Our results show convergent evolution of elevational shifts across clades. Low elevation habitats are important not only for conserving low elevation birds but also for conserving wintering sites of most high elevation breeders.

KEYWORDS

community science, diet, eBird, elevational migration, life history, movement ecology, thermal regime

1 | INTRODUCTION

Large elevational gradients have starkly different environmental conditions at their extremes although the physical distances separating them are very small compared to latitudinal gradients (Rahbek et al., 2019). Many animals move along elevational gradients seasonally. Such seasonal elevational migration has independently evolved across multiple taxa and is a geographically and phylogenetically widespread behaviour (Hsiung et al., 2018; Williamson & Witt, 2021). It is particularly common in birds and has been documented in at least 12% of all species (Barcante et al., 2017). Macroecological (continent-wide) patterns in the extent and timing of latitudinal migration are known (Briedis et al., 2020; Rushing et al., 2020), but elevational movements at the scale of a large montane avifauna have not been studied in detail (Somveille et al., 2013; but see Tsai et al., 2020). Montane avian assemblages arise through independent colonization of the highlands by species belonging to distinct taxonomic genera or families (Fjeldså et al., 2012; Rahbek et al., 2019). Therefore, uncovering patterns in the extent of seasonal elevational shifts is important to understand convergent strategies across taxonomic scales towards a montane life history.

Temperate mountains experience strong seasonality, especially at high elevations, with cold winters and warm summers. Avian downslope movements in winter may be driven by mechanisms associated with cold temperatures such as food limitation (Elsen, Kalyanaraman, et al., 2016; Ketterson & Nolan, 1976; O'Neill & Parker, 1978) and physiological limitations on thermoregulatory ability such as metabolic flexibility (Stager et al., 2016) or insulative plumage (Barve et al., 2021). Birds may shift upslope in the summer to exploit nesting opportunities (Boyle, 2008a; Green et al., 2015) or track pulses in arthropods and other food (Boyle, 2008b; Paxton et al., 2020; Supriya et al., 2019). The large temperature variation in temperate mountains may bring about patterns in elevational shifts similar to latitudinal migration, with montane species generally breeding at high elevations and spending the winter at lower elevations (Borras et al., 2010; Garwood et al., 2009; Ishtiaq & Barve, 2018). However, it is important to note that both latitudinal and elevational migration are not independent of each other and is often a matter of the degree to which a species may move along either axis. In this study, we consider elevational migration as the case where bird species seasonally shift elevations along an elevational gradient that does not vary significantly in latitude.

Research on latitudinal migration has uncovered two patterns that are especially pertinent to elevational migration. (1) Some latitudinal migratory birds move within relatively narrow temperature ranges, matching the thermal conditions between breeding and non-breeding (henceforth winter) seasons, even more closely than resident species (Gómez et al., 2016; Malpica & Ornelas, 2014; Papeş et al., 2012; Zurell et al., 2018), while (2) other species switch thermal regimes between the breeding and winter seasons, moving to habitats with disparate thermal conditions across seasons (Dufour et al., 2020; Laube et al., 2015; Nakazawa et al., 2004; Ponti et al., 2020). Somveille et al. (2019) further demonstrated that birds

that track temperature regimes make up a large proportion of latitudinal migrants and tend to, at a global scale, have shorter migration distances compared to thermal niche switchers. But whether elevational migrants show similar patterns with respect to thermal niche tracking/switching is not widely known.

The extent of seasonal elevational shifts (we use elevational 'shifts' rather than 'migration' since such movements are generally not shown by the entire population (Boyle, 2017) may be driven by factors other than, or in addition to, matching or switching thermal regimes. Although generally involving only short physical distances compared to latitudinal migration, dispersal ability may limit elevational shifts (Sheard et al., 2020). Avian foraging guilds have also been linked to elevational shifts (Pageau et al., 2020). Since arthropods, fruits and nectar resources are scant at high elevations in the winter, invertivores, frugivores and nectarivores are expected to shift further downslope than other foraging guilds such as omnivores or granivores (Pageau et al., 2020).

The large elevational gradient and the hyper-diverse bird assemblage (Price et al., 2014) of the Himalayas allows us to test several novel hypotheses about the drivers of distributional shifts along elevational gradients. At high elevations (>2500m) in the Himalayas, as many as 70% of the species show downhill elevational movements in the winter (Dixit et al., 2016) with significant variation in the elevational extent of shift within and across species (Norbu et al., 2013; Williamson & Witt, 2021). Seasonal elevational shifts are thus a dominant life-history strategy in Himalayan birds.

Himalayan bird elevational shifts may show one of four potential patterns (Figure 1). (A) Species that shift the most have the

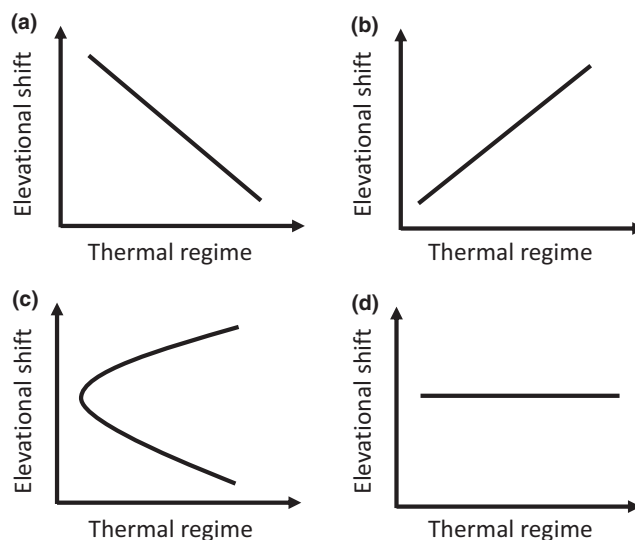


FIGURE 1 Four potential patterns of elevational shift based on species matching or switching their elevational thermal regimes. (a) Taxa with the greatest shift have the narrowest thermal regime (niche tracking), (b) taxa with the greatest shift have the widest thermal regime (niche switching), (c) taxa with smallest and greatest shifts have the widest thermal regimes (intermediate shifts have the narrowest thermal regimes (Somveille et al., 2019)) and (d) no relationship between elevational shift and thermal regime.

narrowest thermal regime by tracking thermal conditions across the breeding and non-breeding seasons (in other words, a negative relationship between extent of elevational shift and width of thermal regime), (B) species that shift the most switch thermal regimes across seasons, a positive association between elevational shift and thermal regime; or (C) taxa with the narrowest thermal regimes have intermediate shifts (niche tracking), while species with wide thermal regimes move the least (high elevation residents) or the most (niche switching) (Somveille et al., 2019). However, (D) elevational shift may not be driven by thermal regime at all, but instead driven by other life-history traits such as dispersal ability or diet.

The biogeography of the Himalayan avifauna predicts potential differences in elevational shift in the eastern versus the western Himalayas. The eastern Himalayas have almost twice the number of species and are relatively aseasonal compared to the western Himalayas (Price et al., 2011). However, these differences are greatest when comparing low elevations (<1000m) in the east and the west. High elevation habitats (>2500m) have communities that are similar across the mountain system (Price et al., 2011). Higher species richness and the resulting high interspecific competition due to species packing is expected to lead to narrower species thermal regimes (more structured communities) in the east (Price et al., 2014; Srinivasan et al., 2018), while increased seasonality and low species richness are predicted to select for broader thermal regimes in the west. Thus, for species found in both the eastern and western Himalayas, thermal regimes are predicted to be broader and elevational shift greater in the west when compared to the east (Table 1; Chan et al., 2016; Srinivasan et al., 2018).

In this study, we used the large and growing community science driven species occurrence database eBird (Sullivan et al., 2014) to model the extent of elevational movement of Himalayan bird species. Using this comprehensive data set (following robust filtering approaches to account for biases) and geo-spatial temperature data, we tested whether thermal regime, dispersal ability and diet drive avian elevational shifts across the Himalayas.

2 | MATERIALS AND METHODS

2.1 | Data collation and cleaning

eBird is the largest data set of direct observations of birds by community scientists. eBird checklists have extensive spatio-temporal coverage of the elevational gradient throughout the Himalayas (Figure 2) and thus represent a robust data set to understand avian

elevational distribution. To compile our Himalayan bird data set, we downloaded eBird observations from Bhutan and India (states of Jammu and Kashmir, Ladakh, Himachal Pradesh, Uttarakhand, Sikkim, West Bengal and Arunachal Pradesh) from all points in the past up to August 2022. Next, to retain only those observations made in the Himalayas, we subset the data set to the latitudinal and longitudinal extent of the Himalayas. The biotic and abiotic differences between the eastern and western Himalayas likely influence the extent of elevational migration in birds (Srinivasan et al., 2018). We thus analysed the checklist data separately for the eastern (Sikkim, North Bengal, Bhutan, Arunachal Pradesh) and western (Jammu and Kashmir, Ladakh, Uttarakhand, Himachal Pradesh) Himalayan zones. Following (Johnston et al., 2021) we considered only 'complete' checklists (i.e. those checklists in which all birds seen or heard by an observer were documented) and further subset the data to only include those checklists that had a distance effort of less than 2.5 kilometres and temporal effort of less than 120min to ensure accuracy of elevation data. We further included only checklists from May to August and December to February, considered to be breeding (summer) and non-breeding (winter) months respectively.

2.2 | Calculating extent of elevational shifts

We quantified the difference between breeding and non-breeding elevations as a measure of the elevational shifts in a species. Towards this goal, we first extracted the elevation associated with each checklist from the SRTM Digital Elevation Model which has a resolution of 1 km (Farr et al., 2007). Since the number of checklists was uneven across elevations and seasons, the estimated elevational distribution of a species may be skewed towards the elevations with more checklists. To account for this sampling bias, we used a resampling protocol described by Tsai et al. (2020). We divided the Himalayas into seven 500-m elevation bands (Tsai et al., 2020). Due to low sampling effort and since the highest elevations sampled in the summer and winter for both the eastern and western Himalayas are not very different (east-winter: 5152m, east-summer: 5397, west-winter: 5150, west-summer: 5879), all eBird checklists above 3000m were pooled together (see Appendix S1 in Supporting Information; Table S1.1). We resampled checklists with replacement and made sampling effort (number of checklists) equal across every combination of elevation band and season. This was repeated for three different levels of sampling effort which correspond to the first, second and third quartiles (east: 453, 611, 811; west: 1357, 2667, 2928). Resampling was

TABLE 1 Table of predictions for species elevation shift and thermal regime based on variations in seasonality and competition they may experience in the eastern and western Himalayas.

	Factor	Elevation shift	Thermal regime
Eastern Himalayas	Low seasonality	Smaller	Narrower
	High species richness	Smaller	Narrower
Western Himalayas	High seasonality	Larger	Broader
	Low species richness	Larger	Broader

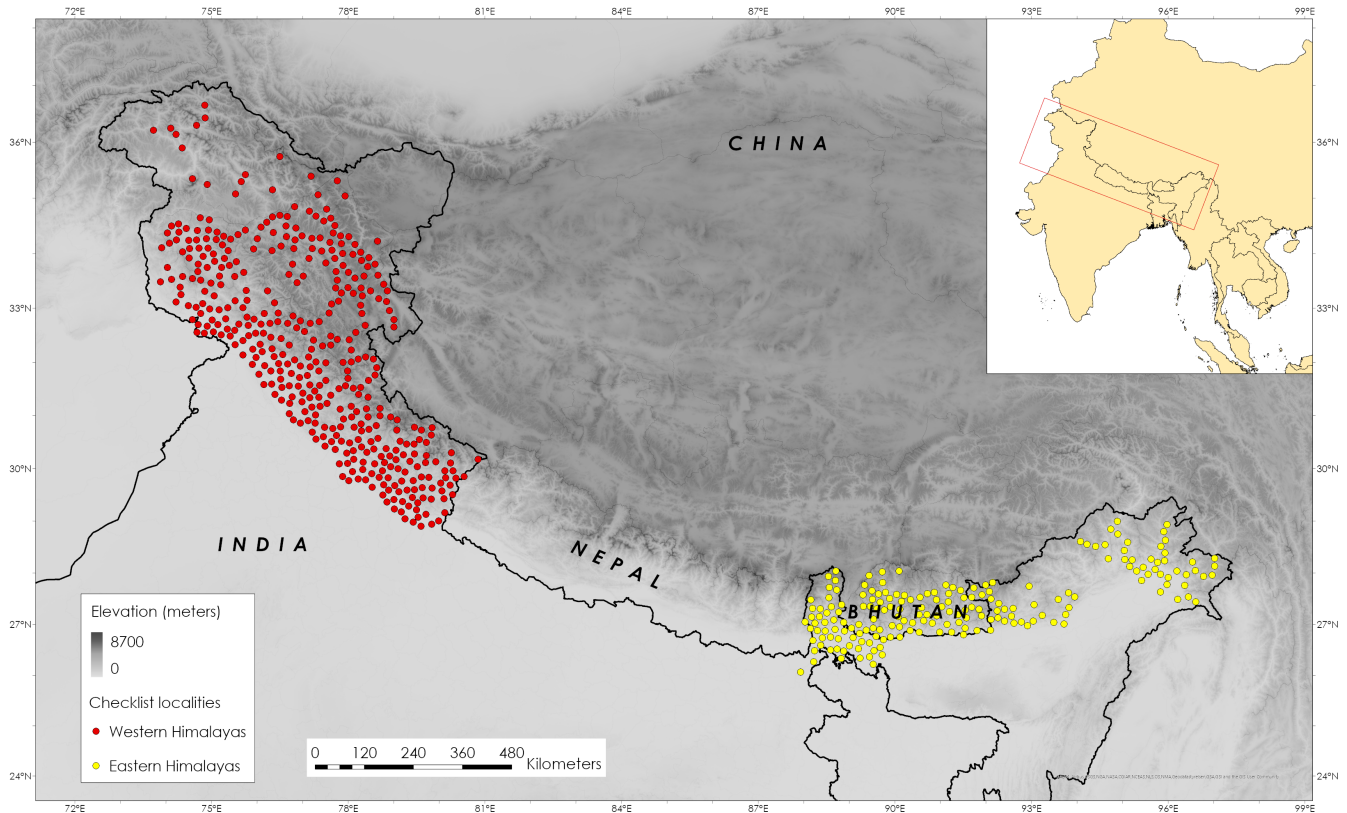


FIGURE 2 Map showing sampling points included in our data set for elevational migration in Himalayan birds. For ease of visualization, we spatially thinned localities to show only 710 unique locations, by ensuring a minimum distance of 15 kilometres between each checklist locality. This process was carried using the *thin* function from the *spThin* package within the R programming environment (Aiello-Lammens et al., 2019; R Core Team, 2021). This map was created in ArcGIS Pro with a shaded relief from a high-resolution digital elevation model (SRTM).

then repeated 1000 times (Tsai et al., 2020) to produce a robust estimate of the elevational distribution for each species in each season and region. For each set of resampled checklists, we calculated the median (50th percentile) elevation where a species was recorded in the breeding and non-breeding seasons to represent the centre of the species' elevational distribution in each season. We similarly calculated the 95th and 5th percentiles to represent species' upper and lower elevational distribution boundaries, respectively, in each season. To avoid biased elevation ranges for rare species and/or species with a low number of detections, from each resampled set, we only retained those species with at least 30 occurrences across all elevational bands in each of the two seasons. Since the selection of species with 30 occurrences was arbitrary, we also repeated the analysis with a 60 occurrence criterion to ensure reliability of our estimates (following Tsai et al., 2020). Given that altitudinal and latitudinal movement can be intricately linked, we include only terrestrial bird species that are known to breed in the Himalayas and move along the Himalayan elevational gradient (Billerman et al., 2020). We did not include raptors (*Accipitriformes*), swifts (*Apodiformes*), swallows (*Hirundinidae*) and falcons (*Falconidae*), since the observations of these birds are generally made when they are in flight and thus estimating elevation can be prone to errors.

To quantify the magnitude of elevational movement, we measured the difference between the breeding and non-breeding elevation (centre, upper and lower boundary) of a species. We classified each species as a downslope or upslope migrant if the 95% confidence interval of the difference in the centre or either boundary (upper or lower) of a species distribution obtained from the 1000 resamples was completely above or below zero respectively (Tsai et al., 2020). If the 95% confidence intervals overlapped zero, we categorized the species as a likely non-migrant. However, it must be noted that there are a few inherent biases associated with community science data (Johnston et al., 2021; Kosmala et al., 2016; Shen et al., 2023) and with more/finer scale data, it is possible that species classified as non-migrants in this study may actually show some level of altitudinal migration.

2.3 | Thermal regime

We calculated the thermal regime (the intra-annual range of temperatures a species experiences) for all species separately in the east and the west Himalayan zones. To do this, we first subdivided the Himalayas into western and eastern Himalayas (see previous section). Next, we downloaded four climatic predictors, each representing the

maximum and minimum temperature for January (considered as peak winter) and June (considered as peak summer) from CHELSA at a spatial scale of 1 km (Karger et al., 2017) separately for the east and west. Then, for every 100-m elevational band, we calculated mean minimum temperatures in January (coldest month) and mean maximum temperatures in June (warmest month) for each zone (western and eastern Himalayas). For each species, we calculated the thermal regime as the difference between the mean maximum June temperature at the species' breeding elevation and the mean minimum January temperature at the species' wintering elevation (separately for the centre, lower and upper boundary of a species' elevation distribution).

2.4 | Statistical analyses

The following analyses were done separately for the eastern and western Himalayan zones. We tested if thermal regime, dispersal ability and diet significantly drive Himalayan bird elevational shifts using a phylogenetic generalized least squares regression (PGLS, Revell, 2010) (Table 1). *p*-values were adjusted for false discovery rate using the Benjamini–Hochberg correction. We assigned dispersal ability (the Hand-Wing Index of the species, a commonly used proxy for dispersal ability in birds; Sheard et al., 2020), and diet guild as either fruits, seeds, invertebrates, vertebrates, and omnivores to each species from the global data set in Sheard et al. (2020)). We recognize that high elevation species have the opportunity for much larger downslope shifts than low elevation species; however, we find a very weak relationship between relative elevational shift (elevation shift/breeding elevation) and breeding elevation (Table S1.2). This shows that elevational shifts were not affected by geometric constraints, and are driven by mechanisms beyond the elevation available for movement in the Himalayas.

For the species that were common to both data sets (east and west Himalayas), we conducted a phylogenetic paired *t*-test using the package 'phytools' (Revell, 2012) to investigate whether the same species had significantly different extent of elevational shift or thermal regime in the east compared to the west. In all models, we controlled for phylogenetic effects by including a phylogenetic correlation matrix as a random effect using the statistical package *ape*, *phangorn* and *nlme* (Paradis et al., 2004; Pinheiro et al., 2017; Schliep, 2011). The phylogenetic correlation matrix was created from a maximum clade credibility tree derived from 1000 phylogenetic trees ('Hackett All Species' backbone) downloaded from <http://birdtree.org> (Jetz et al., 2012). All analyses were done in the programming environment R v. 4.0.2 (R Core Team, 2021).

3 | RESULTS

We analysed data from 47,936 eBird checklists (2011 to 2022) from the Himalayas (east = 9992 and west = 37,944) to model the breeding and non-breeding elevational distribution of 302 species. Results outlined below are for analyses with data from the highest sampling effort (east: 811; west: 2928) and the 30 occurrence criterion. In the

eastern Himalayas, we recovered elevational distribution data for 198 species; 55%, 59% and 56% ($n = 108, 117, 111$) species showed a significant downslope shift at their lower, median and upper elevational limits, while 10% ($n = 20, 20, 19$) showed upslope shifts, and 35%, 31%, and 34% ($n = 70, 61, 68$) species showed no shifts across seasons. Species shifting upslope were typically lower elevation birds (mean of median summer elevation \pm SE = $1005.5 \pm 174.2.0$ m and mean of median winter elevation = 1218.5 ± 170.9 m). In the western Himalayas, we recovered data for 221 species; 57%, 65% and 64% ($n = 126, 144, 142$) of species showed downslope shifts at their lower, median, and upper limits; 5%, 4% and 5% ($n = 10, 9, 10$) of species showed upslope shifts, while 38%, 31% and 31% ($n = 85, 68, 69$) species showed no elevational shifts. In the west, like in the east, species shifting upslope were lower elevation birds (mean of median summer elevation \pm SE = 1076.11 ± 226.5 m and winter 1230.5 ± 214.26 m).

3.1 | Association between elevational shift and life history

In both the east and the west, elevational shift had a significant negative association with thermal regime across all sampling efforts and at the lower, median and upper elevational limits (Figure 3a–c, Tables S1.3 and S1.4). However, in both the eastern and western Himalayas, the absolute value of species thermal regime was never zero and ranged between 10 and 30°C. After accounting for thermal regime, we found that diet had a significant effect on the extent of elevational shift while species' dispersal ability (hand-wing index) did not (Figure 3c, Tables S1.3 and S1.4). Compared to invertivores, frugivores shifted shorter distances which was statistically significant at the median limit in the western Himalayas and all three limits in the eastern Himalayas (Figure 3b). In the eastern Himalayas, granivores shifted further downslope which was significant at their lower limit while omnivores shifted shorter distances downslope which was significant at their upper limit. Invertivores and granivores on average shifted farther downslope than omnivores and frugivores (Figure S1.1).

We recovered 117 species common to both the east and the west. Elevational shift was significantly greater in the west than the east only at the median elevational limit (Figure 4a and Table S1.5). Birds moved within significantly narrower thermal regimes in the east than in the west across all elevational limits and sampling efforts (Figure 4b and Table S1.6).

4 | DISCUSSION

We used a global community science data set to unpack patterns in avian elevational shifts along the world's largest elevational gradient. Around 65% of the species in both the eastern and western Himalayas showed seasonal elevational shifts which is within the range of species reported for other bird communities around the

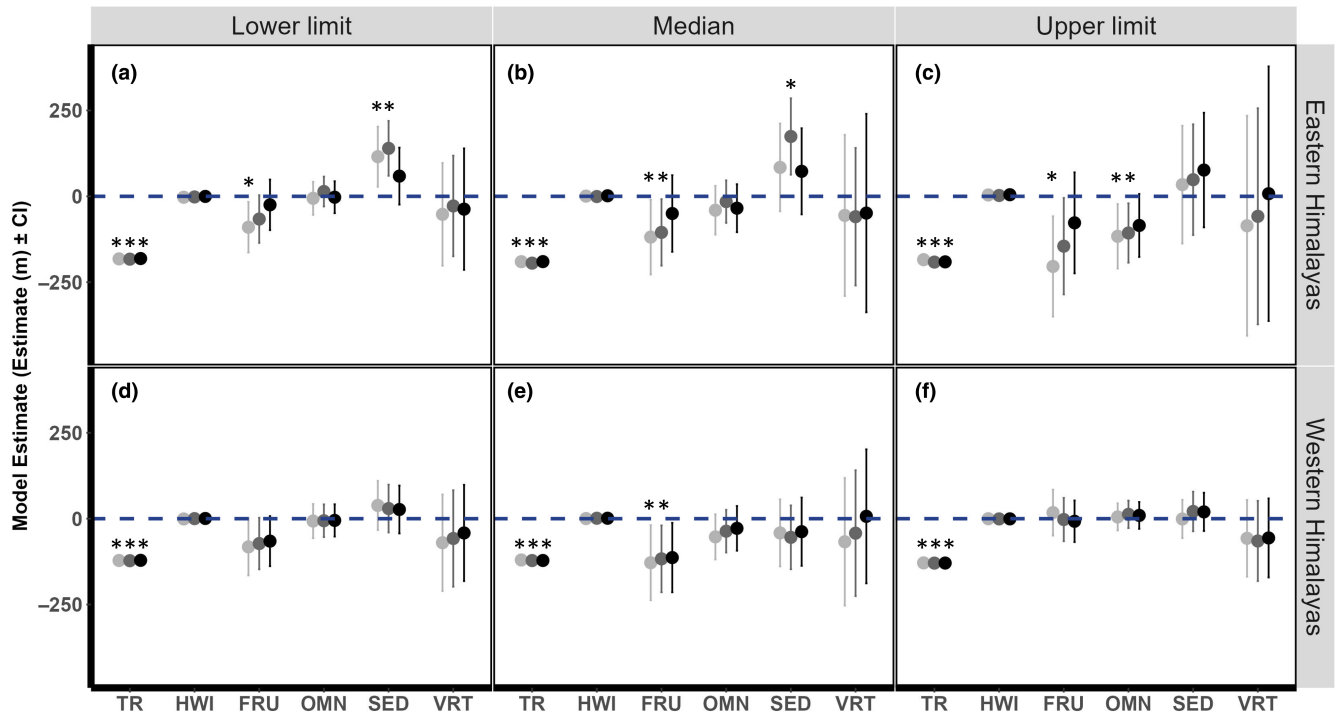


FIGURE 3 Determinants of elevational shift in east Himalayan birds (top panel) and western Himalayan birds (bottom panel). Asterisks denote significant ($p < 0.05$) differences using the Benjamini-Hochberg correction. Dots represent model estimate and errors bars denote 95% confidence intervals for PGLS models used in the comparative analyses. Colour of the dot represents sampling effort (light grey: low, dark grey: medium and black: high); thermal regime (TR), dispersal ability (HWI) and diet (FRU, frugivores; OMN, omnivores; SED, seed eaters; VRT, vertivores). Within diet classes, reference level is invertivorous diet.

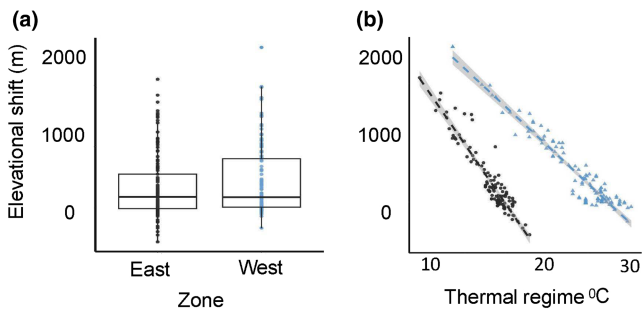


FIGURE 4 For common species across the eastern and western Himalayas, (a) Seasonal elevational shift is significantly greater in the west (blue circles) versus the east at the median elevational limit (black circles) (Phylogenetic paired t -test, $p < 0.05$). (b) Thermal regime is narrower in the east (black circles) for all species compared to the west (blue triangles) ($p < 0.05$).

world (10%–70%) and similar to what was previously reported in the Himalayas (Boyle, 2017). The species that showed the greatest shifts tended to be species that breed at the highest elevations.

4.1 | Tracking thermal niches: Comparisons to latitudinal migration

With species moving seasonally upslope in the summer and downslope in the winter, elevational migration on mountains with

high seasonality may have parallels to latitudinal migration (Hsiung et al., 2018). Throughout the Holarctic, very few high latitude breeders are resident all year round (Newton & Dale, 1996a, 1996b). Similarly, in the Himalayas, most species that breed at high elevations do not over-winter there (Dixit et al., 2016; Katuwal et al., 2016). In our data set, in the east, only 4 out of 37 species (*Urocissa flavirostris*, *Dendrocopos darjellensis*, *Garrulax ocellatus* and *Alcippe vinipectus*) with summer median elevational limit above 2500m showed no shift or a slight upslope shift, while no species in the west breeding above 2500m were resident or showed upslope shifts. Globally, most latitudinal migrants move short or intermediate distances to track their summer thermal regime in their winter distribution (Somveille et al., 2019; Zurell et al., 2018), while others migrate long distances to environments with considerably disparate thermal regimes (Salewski & Jones, 2006). If elevational migration showed a similar relationship between elevational shift and thermal regime, we would have observed a 'C'-shaped association (Figure 1c). Using the elevational temperature profile data, we find that species would have to migrate more than 4000m to start switching their thermal regime; however, we do not find any species performing such a large elevational shift (maximum: ~3000m). Our results suggest that Himalayan bird species that shift the most, track thermal regimes most closely and are thus represented by the pattern in Figure 1a. In other words, species that move the most have the narrowest thermal regime (smallest difference between summer high and winter low).

However, due to other factors like diet and habitat preference, these species do not match their breeding range temperatures as closely as possible (by migrating to the lowest available elevation) and will winter at sites that are colder in the winter, than the minimum temperature at their breeding elevation in the summer. For example, Buff-barred Warbler *Phylloscopus pulcher* migrates nearly 1900 m downslope from 3700 m to 1800 m and, while theoretically it could move further down to better match its breeding range temperatures, diet and habitat preferences may prevent it from doing so. Since elevational movements are relatively short distance, elevational shifts correspond to the wider result of birds moving short distances to track thermal regimes. Why this pattern of elevational shift arises repeatedly across distantly related taxa found in the same mountain system is difficult to say based on our data. There may however be survival trade-offs between the effort of seasonally moving into low elevation communities that are more species rich and hence have higher interspecific competition, versus coping with cold temperatures and low food availability in the winter. For example, birds tracking thermal regimes across seasons may have increased survival during the winter compared to species that shift shorter distances and endure colder winters (Winger & Pegan, 2021). This can in turn lead to the repeated selection for thermal regime tracking in high elevation species. We restricted this analysis to birds that move within the Himalayas. However, there are several species that breed at high elevations in the Himalayas but migrate latitudinally to southern India (e.g. taxa in Phylloscopidae, Muscicapidae; Williamson & Witt, 2021). Future research should seek to understand if these species, as Somveille et al. (2019) predict, switch thermal regimes during winter and exploit more resource rich habitats by moving farther away, both elevationally and latitudinally.

4.2 | Other determinants of elevational shift

Diet has been shown to drive the extent of elevational movement in birds around the globe (Barcante et al., 2017; Pageau et al., 2020). Low temperatures in winter likely result in low food availability for frugivores, nectarivores (Quitián et al., 2018) or invertivores (Supriya et al., 2019). High elevations support higher arthropod abundance, fruit and nectar resources in the breeding season than low elevations (Ghosh-Harihar, 2013; Supriya et al., 2019). We found that diet provides some explanation for the extent of elevational shift in birds especially in the eastern Himalayas. Invertivores and granivores shifted further downslope than frugivores and omnivores suggesting that insect resources and seeds might be limiting at higher elevations in the winter and not fruit resources. Omnivores being dietary generalists can access a variety of dietary items and need not migrate (Resano-Mayor et al., 2019). Food supplementation experiments may help reveal the relative importance of diet and temperatures on elevational shifts in montane birds. Previous research has shown that food availability does drive variation in elevational distribution in the winter (Gross & Price, 2000) and food subsidies

due to anthropogenic habitat alterations do change elevational shift patterns (Elsen, Tingley, et al., 2016).

4.3 | Comparisons to other elevational movement studies

We used methods similar to Tsai et al. (2020) and report a comparable percentage of elevational migrants, ~65% in the Himalayas and ~60% in Taiwan. While the effect of climate was measured differently in both studies, the results complement each other by suggesting that birds that migrate the most remain within narrow thermal niches because, as Tsai et al. (2020) found, they may have a narrower thermal tolerance range. While in Taiwan they find frugivory and insectivory to be significant predictors of elevation shifts, in the Himalayas we find that frugivores move the least while invertivores move significantly farther downslope. This result may be due to the lack of high elevation frugivores in the Himalayas. Like results in Tsai et al. (2020), Liang et al. (2021) and Boyle (2017), we also found that around 10% of all species (largely breeding below 1500 m) showed significant upslope shifts of several hundred metres in the winter. This surprisingly consistent result across passerine and non-passerine taxa, and mountain systems, suggests that upslope movement is a seemingly counterintuitive, but common movement pattern in lowland montane birds. Whether these movements are driven by interspecific competition with over-wintering latitudinal migrants at low elevations, unknown variation in food resource phenology (Barcante et al., 2017; Tsai et al., 2020), or specifically within the Himalayas, by birds moving in from colder areas further north-west, remains to be studied.

4.4 | Differences in elevational shift ecology between the eastern and western Himalayas

There were 117 species in common between the eastern and western Himalayas. The overall elevational shift in these common species is significantly different at the median elevational limit, where shifts are greater in the west than in the east, as predicted by the greater seasonality in the west. Yet, differences in elevational shift vary considerably for certain species (Whistler's Warbler *Phylloscopus whistlerii* shifts 553 m more in the west than in the east, while Buff-barred Warbler *Phylloscopus pulcher* shifts 935 m more in the east than in the west, Table S1.7). These differences may be for multiple reasons: (a) the temperature profiles along eastern and western gradients are likely different, (b) the tree line is typically higher in the east than the west (Price et al., 2011) and thus available habitat may vary in elevation in the east and the west, (c) there may be intraspecific ecological differences affected by factors such as resources, habitat and interspecific competition between the two mountain ranges or (d) in certain cases small differences can be attributed to sampling bias due to the nature of the community science data, which is not collected uniformly along the elevation gradient. The

differences between seasonal elevational differences among these species provide fertile grounds for understanding how various abiotic and biotic factors drive species distribution in the Himalayas.

Several other factors are likely to affect elevational shifts, especially at the scale of an entire elevational gradient. Habitat heterogeneity and slope (Katuwal et al., 2016), habitat availability (Elsen, Kalyanaraman, et al., 2016; Srinivasan et al., 2019), ecotones (Terborgh, 1985), the presence of competitors (Barve & Dhondt, 2017) are but a few examples. Srinivasan et al. (2018) showed that species have narrower thermal niches in the eastern versus the western Himalayas likely because of increased interspecific competition. In our data set, we find the same pattern; although migration extent is not greatly different for species common in the east and west, thermal regimes are overall narrower in the east compared to the west. This suggests that species may have either adapted to the more seasonal western Himalayas by broadening their thermal tolerances or high interspecific competition in the east may have resulted in more structured communities, thus leading to narrower thermal regimes.

4.5 | Using community science data to infer shifts

Our analysis was possible because of community science data collected from thousands of locations. We executed careful and exhaustive data cleaning to retain observations made at fine temporal and spatial scales (Johnston et al., 2021) that reflect patterns of distribution in the eastern and western Himalayas similar to those published in other studies (Ali & Ripley, 1983; Bhatt & Joshi, 2011; Dixit et al., 2016; Elsen, Tingley, et al., 2016; Price et al., 2011; White et al., 2019). Furthermore, we used randomization tests to control for variation in the sampling effort across the elevational gradient (Tsai et al., 2020). We understand that the elevational distribution of a species is locally affected by many factors. Thus, in this study, we do not intend to estimate the specific elevational distribution for a species across its entire distributional range in the Himalayas. A community science data set is expected to underestimate the upper elevational limits of species. Yet, upper elevational limits estimated from our study were highly correlated ($t=27.38$, $r=0.85$, $p<0.01$, $df=296$; Table S1.8) with the maximum elevation for that species in the Himalayas in the global data set assembled by Quintero and Jetz (2018). Because our data come from across the Himalayas, we calculated a relatively coarse measure of the intra-annual thermal regime for each species. At the population level, temperatures experienced by species and individuals are likely different. Our results, however, do demonstrate broad patterns in how the elevational distribution of species varies across the year revealing macroecological patterns in elevational shifts driven by high elevation species tracking similar thermal conditions across seasons.

Low elevation species are considered more at risk from land-use changes such as deforestation than high elevation species (Harris et al., 2014; Srinivasan et al., 2019). However, we found that 83% in the east and 79% in the west of all species in our data set have median winter elevations below 2000m. The wintering grounds of high

elevation breeders in the Himalayas are facing one of the fastest rates of land-use change throughout the region (Pandit & Kumar, 2013). Thus, saving low and mid-elevation Himalayan habitats is critical not only for saving species resident at those elevations but also for safeguarding the populations of high elevation birds that spend up to 8 months of the year there in the winter (Menon et al., 2019; Nosedal, 1994; Vázquez-Reyes et al., 2017). High elevation breeders may thus be affected by both local-scale habitat destruction at low elevation and global scale changes such as climate warming in the high elevation breeding ranges. Finding convergent patterns in the extent of elevational migration can help go beyond species level conservation and towards a broader, assemblage level conservation approach across the entire elevational gradient (Elsen et al., 2018).

ACKNOWLEDGEMENTS

We would like to thank all the dedicated citizen scientists who have contributed data to eBird. We would also like to thank Praveen J, Jessie Williamson, Umesh Srinivasan and Jennifer R. B. Miller for discussions on various iterations of this manuscript. This research received no specific grant from any funding agency. TM is supported by the Prime Minister Research Fellowship (PMRF). VR is supported by the Rose Postdoctoral Fellowship at the Cornell Lab of Ornithology. S.B. received support from the Peter Buck Fellowship at the Smithsonian National Museum of Natural History.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data were downloaded from eBird and can be accessed via: <http://ebird.org/data/download>. The data sets generated and analysed during the current study are available on <https://github.com/vjjan91/elevMigration> and are archived on Zenodo <https://zenodo.org/record/8342146>.

ORCID

Tarun Menon  <https://orcid.org/0000-0003-2397-5372>

Vijay Ramesh  <https://orcid.org/0000-0002-0738-8808>

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BIOSKETCHES

Tarun Menon is a PhD student at the Indian Institute of Science and is trying to understand the drivers of elevational movement of birds.

Vijay Ramesh is a Rose Postdoctoral Fellow at the K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology. His research is focused on understanding how the environment shapes the ecology and behaviour of tropical montane birds.

Sahas Barve is an avian ecologist at the Archbold Biological Station (Florida, United States). His research focusses on the evolution of behaviours and morphology mediated by climate and weather events.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Menon, T., Ramesh, V., & Barve, S. (2023). Himalayan birds that show the greatest elevational shifts remain within the narrowest thermal regimes. *Global Ecology and Biogeography*, 32, 2111–2121. <https://doi.org/10.1111/geb.13761>