Precipitation tolerance determines elevational migration strategies of resident birds of the Western Ghats of India.

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Data Accessibility Statement

Raw data was downloaded from eBird and can be accessed by visiting: https://science.ebird.org/en/use-ebird-data/download-ebird-data-products. The source code and data sets utilized in this study are available on https://zenodo.org/records/14291657.

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Abstract:

Aim: Avian elevational migration is a common, but less studied form of short-distance migration. Numerous hypotheses have been proposed to explain this behavior, yet few studies have tested those comprehensively. We examine four non mutually exclusive hypotheses—climatic constraint, limited foraging opportunities, body size, and dispersal ability—using a comparative framework to evaluate their support in explaining avian elevational migration in the monsoon-dominant Western Ghats.

Location: Western Ghats.

Time period: 2013 - 2023.

Major taxa studied: Birds.

Methods: We used citizen science data from eBird to quantify elevational migration patterns of resident birds of the Western Ghats. Using robust data curation and new bias correction methods, we modeled migration patterns of 164 species across summer, monsoon and winter seasons. We built seasonal phylogenetic logistic regression models to test the effect of a species' environmental tolerances, diet, body-size and dispersal ability on elevational migration likelihood.

Results: 43% of resident birds exhibited elevational migration in at least one season. Most species migrated between winter and summer (57), followed by migrations between summer and monsoon (39) and then monsoon and winter (38). Species predominantly moved upslope in summer (82%) and downslope in monsoon (87%), with no discernible pattern in winter. Species with broader temperature tolerances were more likely to migrate across all seasons. Additionally, species associated with wetter environments were more likely to migrate in summer and winter. Lastly, species with narrower precipitation tolerances were more likely to migrate during the monsoon, influenced by diet.

Main conclusions: We find support for the climatic constraint and limited foraging opportunities hypotheses in explaining both the direction and likelihood of elevational migration. Precipitation is a particularly strong climatic driver for elevational migrants, especially under monsoon conditions. This suggests a complex relationship between precipitation tracking and the associated changes in resource availability determining elevational migration strategies in the region.

Key words: citizen science, climatic constraint hypothesis, eBird, elevational migrations, limited foraging opportunities hypothesis, precipitation, species traits.

Introduction

Animal migration is one of nature's most spectacular phenomena, yet we are just beginning to understand the patterns of migration and underlying eco-evolutionary dynamics that determine those patterns. Migration is thought to be favored when the fitness benefits of exploiting spatiotemporally varying resources outweigh the associated costs (Zurell et al., 2018). Migrating animals can take advantage of multiple habitats where suitability (e.g., survival, food availability, predation risk, and reproductive success) differs across seasons and regions (Hsiung et al., 2018; Milner-Gulland et al., 2013). Migration also involves significant costs, such as increased energy expenditure, heightened predation risk during transit, and potentially shorter breeding seasons due to time spent migrating (Alves et al., 2013; Boyle, 2017; Milner-Gulland et al., 2013). These trade-offs influence the evolution of migratory behaviors, where organisms optimize their fitness by balancing the rewards of resource acquisition with the risks and energy costs associated with movement (Bowlin et al., 2010; Shaw, 2016).

While some migrants travel very long distances, many make shorter journeys. Short distance migrants commonly perform seasonal back-and-forth movements between regions with altering favorable and unfavorable conditions, including breeding areas. Short distance migrants are often less time-constrained, thus able to focus on minimizing energetic costs during their seasonal transitions (Dingle & Drake, 2007; Rappole, 2013). Elevational migration is a form of short-distance migration where animals move between breeding and non-breeding grounds that differ in elevation in a cyclical annual pattern (Rappole, 2013). In birds, elevational migration is relatively common, with ~10% of species showing seasonal elevational shifts (Barçante et al., 2017). Although a majority (44%) of avian elevational migrants occur in the neotropics (Barçante et al., 2017), elevational migration occurs worldwide, with, ~ 20% of North American bird species (Boyle, 2017), 55 – 65 % of Himalayan species (Menon et al., 2023), and ~58% of Taiwanese species (Tsai et al., 2021) known to be elevational migrants.

The underlying intrinsic and extrinsic mechanisms explaining elevational migration in birds has been a focus of ornithological research, especially recently (Williamson & Witt, 2021). This has resulted in numerous non-exclusive hypotheses to explain these seasonal elevational shifts. We note four key ones that have garnered empirical support. The first is the 'climatic constraint hypothesis'; here seasonal climatic regimes can expose individuals to unsuitable temperatures, precipitation and wind speeds at their breeding elevations during the non-breeding season. Thus, imposing strong constraints on a species' ability to maintain optimal physiological conditions (Hsiung et al., 2018). To minimize these direct weather-driven physiological constraints, species can move to elevations with more suitable conditions. The central expectation of this hypothesis is that species with narrower tolerances to harsh weather conditions will move downslope during the winter season and upslope during the breeding season to track suitable climate conditions. Recent work by Tsai et al. (2021) and Menon et al. (2023) support this hypothesis and have demonstrated that Taiwanese and Himalayan birds that

are more cold intolerant make larger elevational migrations between their breeding and non-breeding grounds.

Another hypothesis stems from formative work on elevational migrants in the neotropics, where food availability has long been thought to be the driver of seasonal movements of birds (Levey, 1988; Loiselle & Blake, 1991; Stiles, 1988). The limited foraging opportunities (LFO) hypothesis suggests that during heavy wet-season storms, weather-driven reductions in foraging opportunities, not intrinsic food availability, drive taxa with higher foraging needs to migrate to avoid starvation (Boyle, 2008b). This hypothesis, unlike the climatic constraint hypothesis, does not predict that species with narrower climatic tolerances are more likely to migrate. Initial tests of the LFO hypothesis, on the White-ruffed Manakin (*Corapipo altera*) in Costa Rica showed increased captures of elevational migrants at lower elevations following heavy rainfall (Boyle et al., 2010). Community-level studies later confirmed that storms at higher elevations led to a higher abundance of migrants in the lowlands, with body size and diet influencing responses (Boyle, 2011). These studies suggest that species will shift locations to maximize foraging success during periods of poor conditions, indicating an adaptive flexibility in response to changing conditions. In sum, the LFO hypothesis posits an indirect effect of harsh weather on elevational migrants, where species with the greatest foraging need are predicted to make downslope movements during wet seasons to exploit improved foraging opportunities and resource availability. Support exists for both the above hypotheses (i.e. “climate constraint” and “LFO”), the explanatory power of which may depend on system-, season- and species-specific factors. Using a comparative approach across multiple species can provide a means to determine if one or the other (or both) hypotheses are most supported.

Two other hypotheses focus more on intrinsic morphological traits: The first is the ‘body-size hypothesis’, which proposes that larger individuals can better endure severe weather and scarce food resources, and thus should make shorter migrations from high-altitude breeding grounds (Ketterson & Nolan, 1976). The second hypothesis focuses on dispersal ability (Claramunt et al., 2012; Sheard et al., 2020), and posits that better dispersers are likely to show stronger elevational migration. Still, the body of research conducted on avian elevational migration remains limited to shifts between breeding and non-breeding grounds, with little attention to movements over complete annual cycles (but see (Rueda-Uribe et al., 2024). Transitional seasons, between breeding and non-breeding seasons, may pose particular challenges for birds in highly seasonal, tropical systems. Improving our understanding of elevational movements of birds during these transitional seasons could lend further support to traditional hypotheses explaining this complex and understudied behavior.

A significant challenge in studying avian elevational migration over annual cycles is the need for year-round monitoring over broad geographic extents. Citizen science initiatives, such as eBird, can help overcome some of these challenges via assembling semi-structured checklists in a common format submitted by an extensive network of citizen scientists (Kelling et al., 2019; Sullivan et al., 2009). Still, these data resources, however extensively verified or complete,

contain sources of bias including uneven sampling over space and time (Sullivan et al., 2014). In the context of avian elevational migration, biases in citizen science data can skew results towards elevations where sampling has been more frequent. Researchers have employed various statistical methods to correct these biases, specifically resampling bird occurrences within elevational bands to obtain more uniform sampling across elevations (Menon et al., 2023; Tsai et al., 2021). Yet, there is scope for further improvement in correcting biases from semi-structured checklists, in particular to shift from case specific methods to a more generalizable framework.

In this study we used bird occurrence data obtained from the eBird portal to quantify elevational migration of resident birds in the Western Ghats of India and test key hypotheses explaining this migratory behavior. Our overall goals are to (1) quantify elevational migration distance and identify patterns of movement of resident birds of the Western Ghats over a complete annual seasonal cycle, and (2) test the effect of body size, environmental tolerances, dispersal ability and diet on a species' likelihood of being a seasonal elevational migrant, effectively evaluating the expectations of the hypotheses outlined above. These drivers are not mutually exclusive, but rather may interact to affect species' seasonal elevational movements. Thus, we expect species to demonstrate upslope movements in the summer and downslope movements in the winter season, consistent with the expectations of the "climatic constraint hypothesis." Further we expect that an interaction of the LFO and "climatic constraint" hypotheses will provide an explanatory framework for monsoon season elevational movements. Harsh monsoon conditions, with large amounts of rainfall and higher wind speeds, are most likely to limit foraging opportunities in the higher elevations of the Western Ghats. For this reason, we expect species with narrower tolerances to precipitation and wind speed to have a higher likelihood of being an elevational migrant in this season and will likely move towards elevations where resources are more available, i.e., to the lower reaches of the elevational gradient. Further we expect the temperature fluctuations associated with the summer and winter seasons to match the expectations of the "climatic constraint hypothesis." Thus, we expect species with narrower tolerances to temperature to have a higher likelihood of being a seasonal elevational migrant in these seasons. Lastly, we expect species with small body sizes and high dispersal ability to have a higher likelihood of being a seasonal elevational migrant, as per the "body-size" and "dispersal ability" hypotheses. In sum, we expect the four hypotheses outlined above to have varied, yet season- and clade-specific support in this study. Finally, we present a generalizable method for correcting spatial and temporal sampling biases in citizen science data and provide evidence of its effectiveness compared to previous methods.

Materials and Methods

Study site

The Western Ghats are a 2200 km long, ancient mountain range extending along the western coast of the Indian subcontinent, covering tropical latitudes of 8 N - 21 N (Das et al., 2006); and Fig 1a) and form a significant portion of the Western Ghats and Sri Lanka

biodiversity hotspot (Myers et al., 2000). These mountains are topographically, climatically and biologically diverse (Gadgil & Meher - Homji, 1990, Pascal, 1988) and include an elevational gradient of 40 - 2625 m (Fig 1a), with significant temperature variation between the plains and higher elevations (Fig 1b) and lower temperature seasonality than the eastern parts of the subcontinent (Fig 1c). This mountain range also experiences extreme monsoon conditions during the months of June to October as a result of the annual south-west monsoon. The topography of the Western Ghats interacts with the south-west monsoon to create a longitudinal rainfall gradient (Fig 1d), with higher precipitation seasonality in the northern, lower, portions of these hills as compared to the southern, higher parts (Fig 1e).

eBird occurrence records and data filtering.

We downloaded eBird checklist data from India during the time period from 2013 - 2023. We first applied a spatial filter to these data to include checklists that fell within the bounds of the Western Ghats. Next, we filtered these data to include records between March 2013 to March 2023, resulting in 10 full years of occurrence data. The ten years of data were aggregated for all further analysis. We retained occurrence records associated with complete checklists, where observer(s) recorded all identifiable species. To standardize sampling protocol, we included checklists that followed the "stationary" or "traveling" protocols based on the distance moved by the observer. To reduce the variation in sampling effort, checklists with a sampling duration of >5 hours, sampling distance of >1 km and with >10 observers were excluded, following "Best practices for Using eBird Data" (Strimas-Mackey et al., 2020) and Tsai et al. (2021). Furthermore, the dataset was filtered to include only resident species belonging to the orders: *Passeriformes*, *Bucerotiformes*, *Trogoniformes*, *Piciformes*, *Coraciiformes*, *Cuculiformes*, *Psittaciformes*, and *Columbiformes*. We excluded raptors (*Accipitriformes* and *Falconidae*), swifts (*Apodiformes*) and swallows (*Hirundinidae*) since these groups are generally observed in-flight and associating elevation to these records is difficult (Menon et al., 2023; Ramesh et al., 2022). Checklists were assigned a value for season based on the observation month (summer: March – May; monsoon: June – October; Winter: November – February) and elevation of each checklist was obtained from the ASTER Global Digital Elevation Model, at 30 m resolution (Abrams et al., 2020). To account for geographic location uncertainty, elevations were averaged using a 100 m buffer around each checklist location (Tsai et al., 2021) and rounded to two decimal places. Elevation values and season categories were joined to each species' occurrence record resulting in a long-format dataset of species occurrences with associated elevation and season. All data filtering was performed in the programming environment R v. 4.3.3 (R Core Team, 2024), using the packages 'auk' (Strimas-Mackey et al., 2023) and 'sf' (Pebesma, 2018).

Bias correction and method validation

A key challenge of eBird data is spatial sampling bias (Sullivan et al., 2014). eBird checklists are often located closer to roads (Ramesh et al., 2022), lower elevations are sampled more often than higher elevations (Menon et al., 2023; Tsai et al., 2021) and sampling is

seasonally biased as well. We examined the distribution of occurrence records and checklists as a function of elevation and season to understand sampling effort across our dataset. Sampling was uneven across elevations and seasons; the majority of occurrence records were reported from elevations below 1200 m (Figure S1.1a) and sampling was significantly higher in the winter when conditions are most pleasant (Figure S1.1b). This elevational and seasonal bias in reporting has the potential to skew migration quantifications towards the lower elevations with more robust estimates for the winter. To account for this bias, we developed a resampling approach that helps correct for these issues. We first calculated the cumulative minutes of sampling for each season/elevation combination in our filtered dataset as a measure of sampling effort. We then fit Generalized Additive Models (GAMs; Hastie & Tibshirani, 1986) for each season to predict sampling effort across the elevational range of occurrence records in our dataset. GAMs were built using the 'mgcv' (Wood, 2017) package in the R programming environment. Next, we resampled each species – season combination 20,000 times, with replacement, weighted by the inverse of the predicted value of sampling effort. We used the inverse of sampling effort to up-sample elevations with lower effort and down-sample elevations with higher effort. This resampling approach provides continuous elevational distributions of each species per season under more equal sampling effort. Using this bias adjusted distribution we extracted each species' median (50th percentile) elevation per season. Species with fewer than 10 occurrence records for any one season were excluded.

To test the effectiveness of our approach, we validated our method against the effort correction protocol used in Tsai et al. (2021), who used a different resampling methodology. Briefly, those authors binned sampling effort across elevational band and season and resampled within those bins. In contrast, our approach smooths noise in sampling via fitted GAMs across a continuous range of elevations. Further, we took care to reduce the effect of outliers in our resampling approach by including species with at least 10 occurrence records in each season. We replicated the analyses of Tsai et al. (2021) and then applied our method for bias correction on their data to obtain estimates of median elevation for each species in their study. In comparison, we found that our method produced consistent and reasonably conservative estimates of median elevation (Figure S1.2 & S1.3) and has distinct advantages with respect to execution time (Figure S1.4).

Quantifying elevational migration

We used our method for bias correction on the filtered bird occurrence data and extracted median elevation values for all species in each season. We classified a species as an elevational migrant if the 95% confidence intervals around the median elevation estimate were non-overlapping between two consecutive seasons. This resulted in a binary variable for each season denoting whether a species was an elevational migrant. We then calculated elevational migration distance for a species as the difference between median elevation values between the focal and the previous season. For example, the monsoon season elevational migration distance was calculated as the difference between median elevation in the monsoon and median elevation in

the preceding season, summer ($median_{monsoon} - median_{summer}$). This was repeated for all species and consecutive seasons to arrive at three elevational migration distances per species (Table S1.1).

Species trait data

We calculated each species' tolerance to temperature, precipitation and wind speed in our filtered Western Ghats dataset. To do so, we used the mean monthly temperature, precipitation and wind speed layers, downloaded from CHELSA (Karger et al., 2017), and masked them to the bounds of the Western Ghats. We focused on calculating environmental tolerances within the Western Ghats rather than across a species' global distribution because we were interested in a species' regional adaptations to climate and their associated effect on elevational movements. Next, for each occurrence point of a species in our dataset, we extracted temperature, precipitation and wind speed values from the masked environmental layers. Due to a mismatch between the time period of occurrence records in our dataset (2013 - 2023) and CHELSA data availability (up to 2018), we used CHELSA layers from 2008–2018. We believe this mismatch did not impact our calculations of species' environmental tolerances since we used environmental data across ten years that were matched to our occurrence records to the best of our ability. We calculated each species' 2.5^{th}, 50th (median), and 97.5^{th} percentile values for temperature, precipitation and wind speed using the extracted occurrence specific environmental data. The difference between the 97.5^{th} and 2.5^{th} percentile was considered as the species' environmental tolerance range. Both the tolerance range and median were used as measures of a species' environmental tolerance characteristics in downstream analyses.

Additionally, we extracted body mass (as a proxy for body size), diet preference and Hand-Wing Index (HWI; as a proxy for dispersal ability) from the AVONET global dataset (Tobias et al., 2022). HWI has been shown to be strongly associated with dispersal ability (Sheard et al., 2020), with the expectation that species with long, pointed wings and high HWI have a higher dispersal potential than species with short, rounded wings and low HWI (Claramunt et al., 2012; Freeman et al., 2023).

Statistical analyses

To identify the patterns of movement of species in our study, we used a chi-square test to evaluate the intra-seasonal variation in movement direction (upslope vs downslope). For each season, we calculated the observed frequencies of direction for species demonstrating significant elevational movement and compared these with expected frequencies of equal distribution between direction classes. Chi-square tests were performed using the 'chisq.test' function in R.

We then fit seasonal phylogenetic logistic regression models (Ives & Garland, 2010) to understand the effect of environmental tolerances, body mass, dispersal ability, and diet on a species' elevational migration status. We modeled elevational migration status (migrant or non-migrant) for a given season using a binomial distribution (see the "Quantifying elevational

migration" section above). We performed analyses separately for each season as our expectations were season specific. We employed a backward stepwise model selection approach to select the most parsimonious combination of predictor variables that explain the elevational migration status of a species in a season. We used a consensus Western Ghats bird tree as the basis for determining phylogenetic autocorrelation in our logistic regression models (built using Jetz et al., 2012). The phylogenetic logistic regression model was built using the 'phyloglm' function from the 'phylolm' package (Ho & Ane, 2014) in R and stepwise model selection was performed using the 'phyloglmstep' function from the same package. We also built seasonal Phylogenetic Generalized Least Squares (PGLS) regression models (Revell, 2010) to test the effect of our candidate predictor variables on absolute elevational migration distance (see Table S1.2 for more details).

Results

Patterns of elevational migration

We analyzed 946,282 occurrence records from 105,725 eBird checklists to quantify elevational migration of 164 resident bird species of the Western Ghats over three seasons. Our results revealed that 71 (43%) species showed significant elevational migration in at least one season. Summers had the highest number of elevational migrants with 57 (35%) species, of which 47 displayed upslope movement (Figure 2). This was followed by the monsoon with 39 (24%) species, of which 34 exhibited downslope movements (Figure 2). Winters had a marginally lower number of elevational migrants with 38 (23%) species and did not reveal a clear pattern of movement (Figure 2). Chi-square tests for the summer and monsoon seasons indicated a significant difference in migration direction, with more species demonstrating upslope movements in the summer and downslope movements in the monsoon than expected by chance (Table 1). However, chi-square test results for the winter did not show a statistically significant difference in movement direction (Table 1). We identified only 12 (7%) species that exhibited significant movement in all three seasons, however 34 species were common between the summer and monsoon followed by 26 species between the winter and summer, and 15 species between the monsoon and winter. In sum, our results show a consistent pattern of movement of elevational migrants between the three seasons, with the majority of species moving upslope in the summer and downslope in the monsoon, and no clear or dominant pattern of movement up or downslope in the winter (Figure 2; Figure S1.5).

Association between species traits and elevational migration

Our backward model selection approach for the seasonal phylogenetic logistic regression models shows that temperature and precipitation tolerance characteristics were the strongest predictors of elevational migration status in the summer and winter seasons (Figure 3; Table S1.3). Specifically, we found that summer and winter migration likelihood increased with broader temperature tolerances and an association with wetter conditions (Figure 3; Table S1.3). In contrast, monsoon season models revealed a different set of associations: elevational

migration status was positively associated with temperature tolerance, but negatively associated with precipitation tolerance (Figure 3; Table S1.3). We also found a significant effect of diet in the monsoon season. In particular, frugivorous species were less likely to be elevational migrants, indicating that migration strategies may be influenced by specific dietary needs under monsoon conditions. Lastly, we found no significant association between elevational migration status and wind speed tolerance characteristics, body-size or dispersal ability in any season (Table S1.3).

Elevational migration distance models fit under a PGLS framework, partially aligned with the above results. We found that species associated with wetter conditions performed larger elevational movements in all three seasons (Table S1.2). Additionally, species that moved to a larger elevational extent were associated with higher wind speeds in the monsoon and winter, and had a broader tolerance for temperature in the summer season (Table S1.2). However, these models generally exhibited only modest fit to our data based on adjusted R^2 scores (Table S1.4), and we chose to exclude these from further interpretation.

Discussion

This study quantified the elevational migration strategies of 164 resident bird species in the Western Ghats of India. Utilizing a comprehensive citizen science dataset and robust analytical methods, we identified patterns of elevational movement and tested hypotheses regarding this behavior along one of the world's most biodiverse elevational gradients. Our findings indicate that approximately 41% of resident birds exhibit seasonal elevational movements, a figure comparable to the 44% observed in other tropical regions (Barçante et al., 2017). We found significant directionality in these movements, with species predominantly migrating upslope during the breeding summer and downslope during the monsoon. These strongly consistent movements by nearly all species who make seasonal migrations fit expectations as we discuss below. We more directly tested hypotheses related to climatic constraints and, more indirectly, foraging, via phylogenetically informed logistic regression models. However, the predictions of some of the key hypotheses did not fully align with our results. Surprisingly, we found that species with broader tolerances to temperature were more likely to be elevational migrants, regardless of the season. Furthermore, these species are associated with generally wetter conditions during the summer and winter. Lastly, we found the monsoon season posed significant and unique challenges to elevational migrants. During this season, species with narrower tolerances to precipitation were more likely to be elevational migrants, and these species were less likely to be frugivores. These results suggest that depending on the specific question posed, the season in question, and dietary guild, either the "climatic constraint" or LFO hypotheses may more effectively explain the elevational migration strategies of resident birds in the region.

The first question we addressed is whether there are seasonal variations in the movement direction of elevational migrant species. We identified a clear pattern of movement during the

summer and monsoon seasons. In the breeding summer, the majority of elevational migrants moved upslope from their wintering elevations. Breeding upslope migrations are well documented in species worldwide (Boyle, 2017; Levey, 1988; Menon et al., 2023; Tsai et al., 2021) and are expected under the "climatic constraint hypothesis." Furthermore, evidence suggests that nest predation rates may be lower at higher elevations, as observed in the neotropics (Boyle, 2008a; Skutch, 1985). Therefore, elevational migrants in the Western Ghats may be moving upslope during the breeding summer season to elevations where breeding success is likely to be higher. In the monsoon season, we observed a marked downslope movement of resident birds from their breeding elevations. Heavy and prolonged rainfall - a defining characteristic of the monsoon in the Western Ghats - is known to reduce foraging abilities in small-bodied consumers like birds and bats (Boyle, 2010; Boyle et al., 2020; Foster, 1974; Voigt et al., 2011). Consequently, intense rainfall during the Western Ghats monsoon likely limits foraging opportunities at higher elevations, prompting species to seek refuge at lower elevations where resources are more readily available, consistent with studies examining the elevational response of birds to heavy wet-season storms (Boyle, 2011, 2017; Boyle et al., 2010). This analysis failed to identify a pattern of elevational movement in the winter. Winters in the Western Ghats are the most temperate season, with favorable temperatures across the elevational gradient and limited precipitation. During this season, birds are likely responding to other confounding drivers, like food resource phenology, that were not included in this study. We further tested the drivers of these elevational movements in association with key predictors, as we discuss in more detail below.

Although summer upslope movements may align with breeding site selection and monsoon season downslope movements with the LFO hypothesis, the reasons behind some species moving in unexpected directions remain unclear. For example, the Large Gray Babbler (*Argya malcolmi*), a widely distributed species across the Indian subcontinent (Collar & Robson, 2021), exhibited downslope movement in summer and upslope movement during the monsoon season (Figure 2). Another species, the Palani Laughingthrush (*Montecincla fairbanki*), a range-restricted endemic of the Western Ghats (Collar et al., 2020; Robin et al., 2017), demonstrated a similar pattern of movement (Figure 2). We found eight other species moved downslope in summer and three more species moved upslope during the monsoon season. These species exhibit varied life histories, morphological traits, and range distributions, making it difficult to identify a common driver for these 'against-the-norm' movements through this analysis. We suggest a more species-specific examination of their migration patterns, which could improve understanding of why current hypotheses fail to explain a small subset of species' seasonal elevational movements.

The next question addressed in this study was which factors determine whether a species makes seasonal elevational migration, regardless of direction. Our results support both the "climatic constraint" and LFO hypotheses, depending on the season and variable examined. Species with broader temperature tolerances were more likely to be migratory across all seasons,

which contrasts with the "climatic constraint hypothesis." Recent studies on avian elevational migration in the Himalayas and Taiwan suggest that species with narrower thermal regimes or limited cold tolerance make longer elevational movements (Menon et al., 2023; Tsai et al., 2021), as these regions experience substantial seasonal temperature shifts across steeper gradients. By contrast, the Western Ghats experience low temperature seasonality (Figure 1c), which likely reduces temperature constraints on migratory behavior, allowing species with broader tolerances to remain within a broad thermal niche year-round. This flexibility may allow them to respond to other seasonal drivers, including precipitation patterns, by tracking habitats and resources that fluctuate seasonally. Indeed, we found that precipitation, a climate variable with far greater seasonality than temperature (Figure 1e), had a stronger influence on the likelihood of being migratory. Species favoring wetter conditions were more likely to migrate in both summer and winter, suggesting a tracking of the precipitation dimension of their eco-climatic niche. This result aligns with the "climatic constraint hypothesis," reflecting the need to track wetter regions along the elevational gradient during key breeding (summer) and potentially more resource-limited (winter) seasons. During the monsoon, migrants tended to be species with overall narrower precipitation tolerances, whether they preferred more wet or dry conditions, further supporting the "climatic constraint hypothesis." Collectively, these findings suggest that while temperature constraints are moderate, other seasonal conditions, particularly those varying with precipitation, play a significant role in structuring migratory strategies in the Western Ghats.

Precipitation is known to influence plant and insect phenology (Chown et al., 2011; Mendoza et al., 2017; Newell et al., 2023), which in turn affects food availability for higher trophic levels, providing a potential indirect driver of migratory responses. In the monsoon-dominant Western Ghats, tracking this dimension of a species' eco-climatic niche is crucial for meeting seasonal energy requirements. During the drier seasons (summer and winter), species tend to migrate toward wetter environments where resources may be more abundant. However, during prolonged heavy rainfall events in the monsoon, resources may be abundant but less accessible due to foraging limitations. Consequently, species are likely to avoid areas with excessive precipitation and limited foraging opportunities, favoring lower elevations with more accessible resources. Furthermore, we observed a dietary guild response among monsoon season elevational migrants, with frugivores showing lower odds of migration. On average, frugivorous species in this study were of higher body mass than most other foraging guilds (Figure S1.6), which may make them better equipped to endure resource limitations during the monsoon season (Boyle, 2008b).

In sum, we find strong support for the LFO hypothesis, especially in the monsoon season. Elevational migrants in the Western Ghats appear to track regions of higher precipitation and associated changes in resource abundance during summer and winter. In contrast, larger-bodied frugivores are less likely to migrate during the monsoon, while species that do migrate tend to avoid areas of extreme precipitation where foraging opportunities may be compromised. Our findings reveal the complexity of elevational migration strategies in the region, showing that

species respond to a diverse set of environmental factors, each shifting across seasons in ways that are not always synchronized with breeding periods. These multifaceted and complex relationships may not align with traditional hypotheses, showing how species have adapted to the hypervariable conditions of the Western Ghats.

Caveats and Conclusions:

This work relied solely on citizen science data collected from the Western Ghats by thousands of citizen scientists across India. Despite rigorous filtering, inherent biases persisted (Figure S1.1). We developed an approach to correct these biases by using fitted GAMs to predict sampling effort and resample citizen science occurrence records based on these predictions. The strength of this method lies in resampling across the gradient of occurrence records, weighted by a user-controlled scale of sampling effort. Furthermore, resampling results in a continuous distribution of occurrence records across the gradient of interest. In our case, we applied this method across a gradient of elevation; however, it can be used for various ecological and environmental gradients as long as there is some a priori estimate of sampling effort. We acknowledge that despite bias correction methods, biases in citizen science data may still arise due to its opportunistic nature. For this reason, we did not attempt to estimate the elevational boundaries of a species in this study due to the extremely limited number of high-elevation occurrence records. Instead, we estimated median elevations of a species, which are relatively less prone to error. Further empirical testing of the method is required to ascertain its efficiency in predicting robust estimates of boundary quantiles. By using measures of central tendency, we believe our estimates of species' seasonal median elevation were not influenced by latent sampling biases and were reliable enough for drawing inferences. We also acknowledge that the variables used in our analyses were proxies for traits hypothesized to impact elevational migration, and thus we do not fully or directly test the previously outlined hypotheses. While we provide a reliable foundation for ecological inferences on the drivers of elevational migration, we encourage further research that directly tests these hypotheses, such as quantifying foraging opportunities throughout the year and their impact on elevational migrants or obtaining more direct measures of the physiological tolerances of elevational migrants and their correlation with migratory behavior.

In conclusion, our study highlights the complex drivers behind seasonal elevational migration in the Western Ghats. We found that broader temperature tolerances, rather than narrower ones, were associated with migratory behavior, suggesting that temperature constraints are less impactful in this region. Precipitation, with its greater seasonality and intensity especially during the monsoon season, played a stronger role in shaping migration strategies. Species tended to track wetter regions or avoid extreme rainfall, indicating that resource needs, influenced indirectly by precipitation patterns, drive elevational migration. We also highlight how the monsoon, as a single challenging season, uniquely influences elevational migration strategies throughout the year, driven by factors distinct from those shaping migrations in other

seasons. This emphasizes the importance of including these transition seasons, between the breeding and non-breeding seasons, in future avian elevational migration studies. Summing across seasons, our findings align with both the "climatic constraint" and Limited Foraging Opportunities hypotheses and provide a foundation for further empirical testing of these ideas. The consistent movement of species along the elevational gradient across all three seasons underscores the necessity of preserving these key breeding habitats and elevational refuges to ensure species survival in the region. Given the accelerating land-use changes and biological invasions affecting the Western Ghats (Arasumani et al., 2019; Lele et al., 2020), conserving these vital habitats is essential for maintaining the resilience of bird populations and ensuring the persistence of biodiversity in this ecologically rich area.

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Tables

Table 1: Chi-square test results examining the intra-seasonal variation in elevational migration direction of resident birds of the Western Ghats. Seasonal percentages of species demonstrating downslope (Downslope %) or upslope (Upslope %) movement are reported, along with chi-square statistics (χ^2) and P values for each seasonal test.

Season	Downslope %	Upslope %	χ^2	P value
Summer	18	83	24.018	<0.001
Monsoon	87	13	21.546	<0.001
Winter	53	47	0.105	0.746

Figures

Figure 1: The Western Ghats of India (boundary shown as black line) are topographically and climatically unique. (a) Latitudinal extent and elevational range of the Western Ghats. (b) Mean annual temperature in the region ranges from 12°C at higher elevations to 25°C in the plains. (c) Temperature seasonality is lower along the length of these hills and increases moving eastward across the Indian subcontinent. (d) The Western Ghats creates a strong rain shadow effect, leading to a longitudinal precipitation gradient. (e) The topography of the Western Ghats, results in a decrease in precipitation seasonality moving from north to south. Elevation is built from 30 seconds resolution SRTM data (Farr et al., 2007) and climatic variables are visualized from CHELSA data at 1 km resolution (Karger et al., 2017).

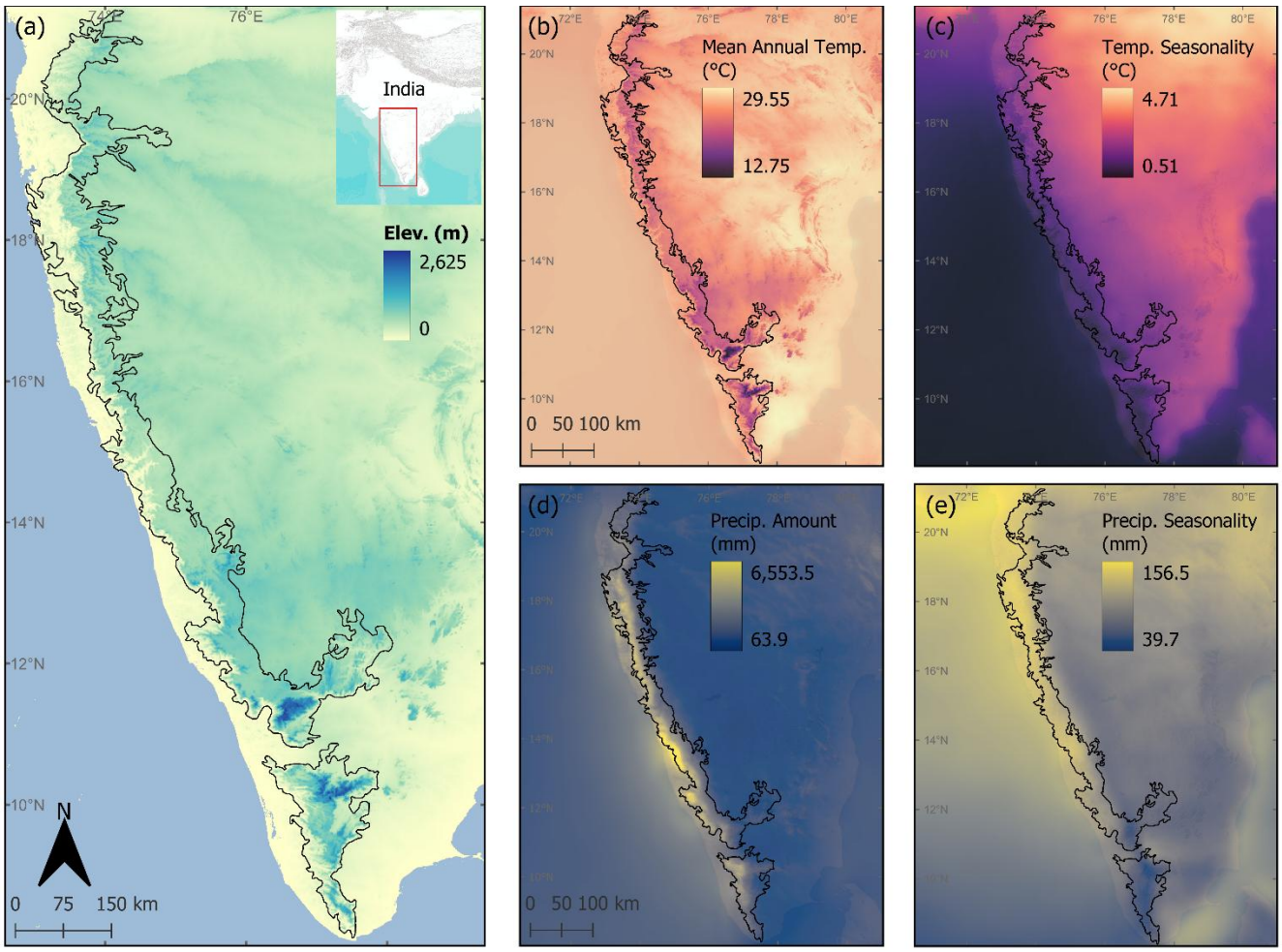

Figure 2: Patterns of elevational migration in this study for species that exhibit significant elevational movement between the seasons of interest. In the summer species moved predominantly upslope followed by downslope movement in the monsoon. The winter saw an almost even distribution of upslope and downslope elevational movements. The distance species move in meters (m) is represented as the length of the arrow.

Summer
Distance (m)
600
500
400
300
200
100
0
-100
Turdus simillimus
Cuculus micropterus
Ducula aenea
Nyctyornis athertoni
Prinia hodgsonii
Lanius schach
Sturnia pagodarum
Merops leschenaulti
Rhipidura albogularis
Cacomantis sonneratii
Cyornis pallidipes
Artamus fuscus
Anthus rufulus
Spilopelia chinensis
Eumyias albicaudatus
Acridotheres fuscus
Motacilla cinerea
Orthotomus sutorius
Argya striata
Parus cinereus
Myophonus horsfieldii
Copsychus saularis
Gymnoris xanthocollis
Argya subrufa
Pellorneum ruficeps
Psittacula cyanocephala
Prinia socialis
Cinnyris lotenius
Pycnonotus luteolus
Pycnonotus jocosus
Cyornis tickelliae
Psilopogon zeylanicus
Psilopogon haemacephalus
Corvus macrorhynchos
Psilopogon viridis
Columba elphinstonii
Zosterops palpebrosus
Pomatorhinus horsfieldii
Passer domesticus
Machlolophus aplonotus
Centropus sinensis
Leptocoma minima
Dicaeum concolor
Psilopogon malabaricus
Eudynamys scolopaceus
Coracias benghalensis
Aegithina nigrolutea
Streptopelia decaocto
Dendrocitta leucogastra
Cinnyris asiaticus
Psittacula krameri
Acridotheres tristis
Argya affinis
Montecincla fairbanki
Dicrurus macrocercus
Dicrurus leucophaeus
Argya malcolmi
Monsoon
Distance (m)
200
100
0
-100
-200
-300
-400
Montecincla fairbanki
Gymnoris xanthocollis
Argya malcolmi
Ficedula nigrorufa
Streptopelia decaocto
Aegithina nigrolutea
Coracias benghalensis
Psilopogon malabaricus
Psilopogon haemacephalus
Zosterops palpebrosus
Machlolophus aplonotus
Centropus sinensis
Dinopium benghalense
Pycnonotus jocosus
Cinnyris lotenius
Psilopogon viridis
Argya subrufa
Dicaeum concolor
Spilopelia chinensis
Pellorneum ruficeps
Copsychus saularis
Passer domesticus
Dendrocitta leucogastra
Orthotomus sutorius
Prinia socialis
Acridotheres fuscus
Parus cinereus
Rhipidura albogularis
Chalcophaps indica
Dicrurus paradiseus
Corvus macrorhynchos
Anthus nilghiriensis
Cacomantis sonneratii
Prinia hodgsonii
Argya striata
Turdus simillimus
Nyctyornis athertoni
Anthus rufulus
Merops leschenaulti
Winter
Distance (m)
200
100
0
-100
-200
-300
-400
-500
Merops leschenaulti
Chalcophaps indica
Anthus nilghiriensis
Argya striata
Anthus rufulus
Corvus macrorhynchos
Dicrurus leucophaeus
Dendrocitta leucogastra
Arachnothera longirostra
Dicrurus paradiseus
Dendrocitta vagabunda
Alcippe poioicephala
Passer domesticus
Argya affinis
Dicaeum concolor
Dicrurus macrocercus
Prinia socialis
Corvus splendens
Picus xanthopygaeus
Eudynamys scolopaceus
Pomatorhinus horsfieldii
Leptocoma minima
Cyornis tickelliae
Psilopogon zeylanicus
Spilopelia chinensis
Myophonus horsfieldii
Artamus fuscus
Lanius vittatus
Lalage melanoptera
Ocyceros griseus
Lanius schach
Motacilla cinerea
Emberiza lathami
Montecincla fairbanki
Gymnoris xanthocollis
Turdus simillimus
Ducula aenea
Cuculus micropterus
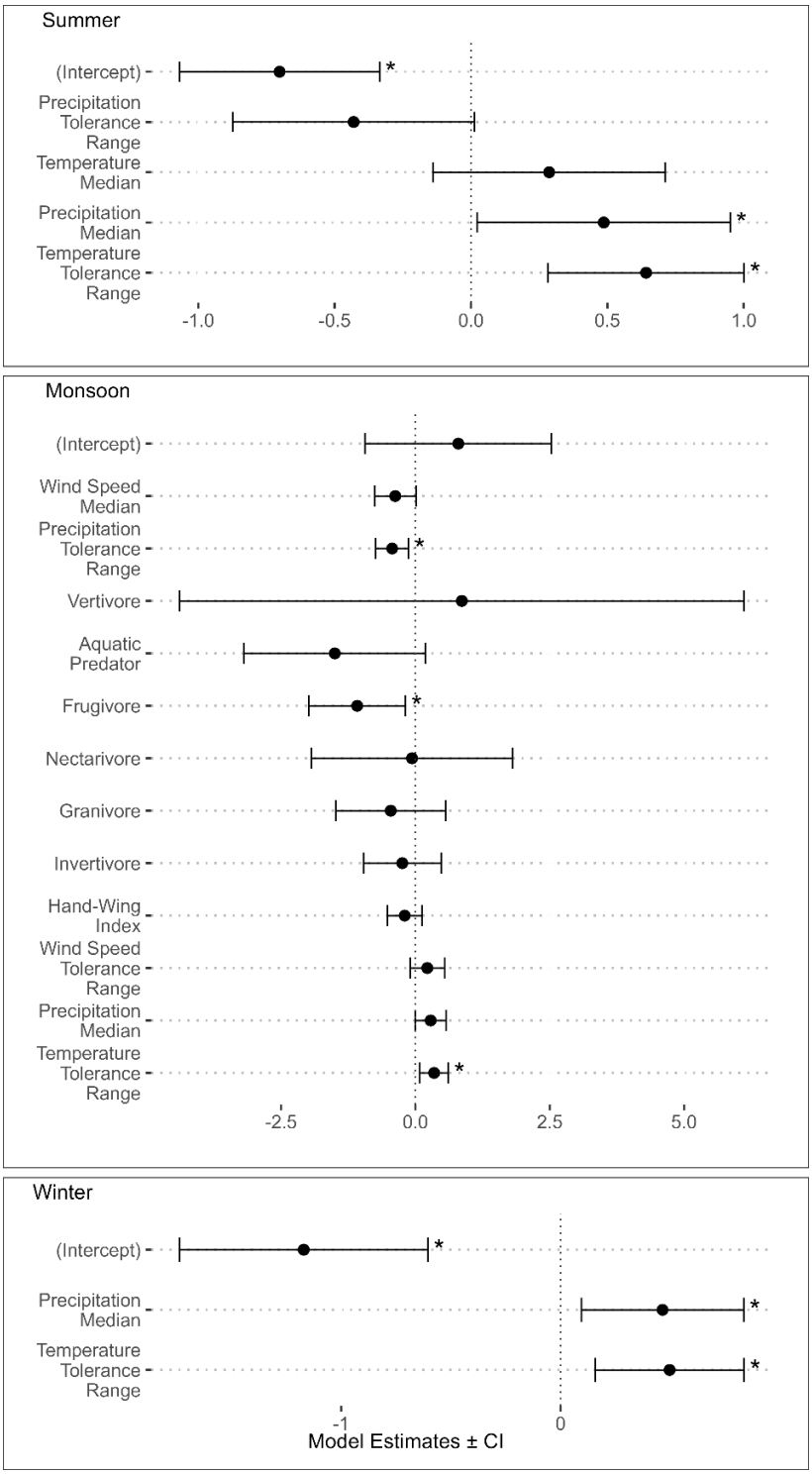
Figure 3: Parameter estimates for our seasonal phylogenetic logistic regression models determining the effect of our candidate predictors on elevational migration status (migrant vs non-migrant). Dots represent model estimates with their 95% confidence intervals as error bars. Asterisk denotes significance ($p < 0.05$). For diet categories, the reference level was set as species with an omnivorous diet.