TEMPORAL NICHE DYNAMICS IN AVIAN COMMUNITIES: AN INTEGRATED ANALYSIS OF SPATIAL, TROPHIC, AND ACOUSTIC PARTITIONING DURING MIGRATION IN THE HIMALAYAN FOOTHILLS

By

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In
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Under the supervision of

Dr.Ashish Jha, Scientist-C

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July 2026

DECLARATION

I hereby declare that the work conducted under the thesis entitled **"Temporal Niche Dynamics in Avian Communities: An Integrated Analysis of Spatial, Trophic, and Acoustic Partitioning during Migration in the Himalayan foothills",** is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of Dr**. Ashish Jha**, **Scientist- C**, of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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CERTIFICATE

This is to certify that the thesis by **Ardra Raju** entitled **"Temporal Niche Dynamics in Avian Communities: An Integrated Analysis of Spatial, Trophic, and Acoustic Partitioning during Migration in the Himalayan foothills"** is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Ardra Raju has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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LIST OF ABBREVIATIONS

AIC- Akaike Information Criterion

asl-above sea level

B′ -Standardized Levins' niche breadth index

BW- Bi-week

df -degrees of freedom

GLMM-Generalized Linear Mixed Model

HB-Himalayan Bulbul

KS-Kolmogorov-Smirnov (test)

LRT-Likelihood Ratio Test

MANOVA-Multivariate Analysis of Variance

NMDS-Non-metric Multidimensional Scaling

NND-Nearest-Neighbour Distance

PCA-Principal Component Analysis

PERMANOVA-Permutational Multivariate Analysis of Variance

PERMDISP-Permutational Analysis of Multivariate Dispersion

RVB-Red-vented Bulbul

RWB- Red-whiskered Bulbul

SD / SE-Standard Deviation / Standard Error

WII-Wildlife Institute of India

THESIS SYNOPSIS

This study examined how resident bird communities respond to the seasonal arrival of migratory birds in the Himalayan foothills. Every winter, large numbers of migratory birds from Central Asia and the higher Himalayas arrive and share habitats and resources with resident species. Despite this annual event, little is known about its effects on resident bird communities. To address this gap, the study was conducted at the Wildlife Institute of India (WII) campus, Dehradun, from December to April, covering the peak migrant season and their departure.

The study investigated resident birds from three perspectives: community composition, foraging ecology, and acoustic niche use. Results showed that while index of species richness remained relatively stable across months, bird abundance index increased during peak migration and declined after migrants departed. Community changes were mainly driven by species turnover, with migrant species replacing one another over time.

Foraging observations of three resident bulbul species revealed that, contrary to expectations, niche breadth increased rather than decreased during periods of high migrant presence. This pattern was likely influenced by seasonal fruit availability, particularly mulberry fruiting, rather than competition with migrants. Morphological and dietary analyses further indicated substantial overlap among the bulbul species.

Acoustic analyses showed that the organisation of bird vocalisations in acoustic space remained remarkably stable despite seasonal changes in species composition.

Overall, the results suggest that the resident bird community at the WII campus is able to accommodate the annual influx of migratory birds without major disruption to its ecological structure. Although species composition and abundance index vary seasonally, patterns of habitat use and acoustic niche organisation remain stable.

This study provides a baseline for understanding resident–migrant interactions in the Himalayan foothills and may help assess future changes associated with climate change and declining migratory bird populations.

1. INTRODUCTION

Avian Communities as Seasonally Dynamic Systems

Bird communities are dynamic systems whose structure, index of species richness, abundance index, composition, and guild representation is continuously shaped by competition, environmental filtering, and dispersal (MacArthur 1960; Chesson 2000). MacArthur's (1960) demonstration that North American warblers partition foraging microhabitat with high precision established that avian communities are structured entities shaped by niche differentiation, not random assemblages. Hutchinson's (1957) multidimensional niche concept formalised the ecological hypervolume each species occupies, while Chesson's (2000) modern coexistence theory showed that community membership at any moment reflects a temporary equilibrium between competitive and environmental forces renegotiated across seasonal cycles. That equilibrium shifts predictably through the year: frugivore-insectivores peak in wet seasons and insectivores at the dry season's end as food resource cycles turn (Malizia 2001), and directional species replacement across seasons is well-documented across taxonomically diverse avian assemblages (Rotenberry and Chandler 1999). Capturing these dynamics requires temporally resolved sampling rather than single-visit snapshots.

Migratory Influx as a Driver of Community Restructuring

Among seasonal forces reshaping avian communities, migratory influx is uniquely disruptive. Nearly one in five bird species globally maintains separate breeding and wintering distributions (Somveille et al. 2013), and their annual movements cause a dramatic, temporary redistribution of avian diversity across the globe. At local scales this translates into a sudden increase in index of species richness and competitive pressure that resident communities must absorb. The mechanisms are well established: interference competition, the direct aggressive exclusion of residents from foraging patches (Marra 2000; Powell et al. 2021), and exploitative competition, the shared depletion of arthropod prey already declining seasonally when migrants arrive (Moore and Yong 1991; Jedlicka et al. 2006). Migrants settle at the worst possible moment for residents: resources are low, arthropod prey is declining, and resident birds are recovering from the energetic demands of breeding (Poulin and Lefebvre 1996). In species-

poor communities this double pressure seasonal resource decline and migrant influx produces especially strong effects on resident populations (Magrach et al. 2020).

At the community level, these competitive dynamics produce measurable shifts in composition, guild structure, and abundance index detectable through multivariate temporal analyses. Guild-level effects are particularly pronounced: insectivorous residents show greater foraging displacement than omnivores in wintering systems, while invertivorous guilds are significantly more likely than generalists to undertake seasonal movements away from areas of migrant concentration (Deppe and Rotenberry 2005; Menon et al. 2025). Competitive dynamics also restructure mutualistic networks plant-frugivore interaction networks reorganise significantly during migration periods, with migrant abundance index and fruit richness together explaining most variance in network structure (Ramos-Robles et al. 2016). At the Himalayan foothills specifically, Srinivasan et al. (2018) showed that competition intensifies during winter in seasonal environments precisely when arthropod prey declines providing theoretical grounding for expecting migrant-driven competitive effects to peak during the dry-season monitoring period of the present study.

Foraging Niche Responses to Migrant Presence

Theory predicts that under strong competition, species narrow their niche use and concentrate on resources they exploit most efficiently, then expand again once the competitor departs a cycle of competitive niche contraction and release (Van Valen 1965; Chesson 2000). Empirical evidence for this cycle is consistent across continents. In a shade-grown coffee plantation in Mexico, Jedlicka et al. (2006) found that a resident insectivore shifted 27% more of its foraging to the understorey when Palearctic migrants were present, coinciding with canopy arthropod depletion and resulting in measurably lower foraging success; the effect was driven entirely by exploitative competition with no direct aggression observed. Gbemiga (2014) in northern Ghana recorded resident birds narrowing their vertical foraging range during migrant presence, increasing overlap among themselves, then spreading out again after migrants departed. Chipley (1976) in Colombia documented six resident species shifting to lower foraging heights upon migrant arrival, with elevated intraspecific aggression suggesting cascading competitive pressure within the resident community. Rabol (1987) found comparable

foraging position shifts and increased migrant aggression toward residents in Kenya as the dry season intensified. Kent and Sherry (2020) demonstrated niche contraction and release across the full migratory season in a Neotropical system, establishing this as one of the clearest ecological signatures of migrant-driven competition.

Not all systems show displacement: where resources are abundant or migrants and residents differ sufficiently in prey size or foraging substrate, partitioning can permit coexistence without resident behavioural adjustment (Salewski et al. 2003; Greenberg 1995; Barbe et al. 2018). The outcome depends on the degree of ecological similarity between the groups involved and on resource scarcity. The more similar the competitors and the scarcer the food, the more likely displacement becomes (Poulin and Lefebvre 1996). The dry season of the Himalayan foothills, when arthropod prey is already declining and millions of insectivorous Palearctic and elevational migrants arrive, represents precisely the conditions under which competitive displacement is most probable.

Omnivorous generalist residents are particularly informative focal species for detecting these shifts because their dietary flexibility means any narrowing of niche breadth can be attributed to competitive pressure rather than simple prey seasonality. Three bulbul species the Red-vented Bulbul (*Pycnonotus cafer*), Red-whiskered Bulbul (*Pycnonotus jocosus*), and Himalayan Bulbul (*Pycnonotus leucogenys*) are abundant year-round residents at the study site that consume insects, fruit, and nectar across seasons. As omnivorous generalists directly overlapping the prey preferences of arriving insectivorous migrants, they are theoretically predicted to show measurable niche contraction during migrant presence and competitive release after departure (Van Valen 1965; Sherry et al. 2016; Kent and Sherry 2020). Their sedentary territorial behaviour and high detectability make them practical subjects for the monthly focal follows on which this study's foraging data depend.

Acoustic Space as a Shared Resource

Migratory influx reorganises communities not only ecologically but communicatively. Sound is a limited resource: when many species vocalise simultaneously at overlapping frequencies, signals mask one another, degrading the communication on which territorial defence and mate attraction depend (Bee

and Micheyl 2008). The Acoustic Niche Hypothesis (Krause 1993) proposes that species partition acoustic space singing at different frequencies, times of day, or with distinct call structures to minimise this interference. Empirical support is substantial: overlap in frequency space is lower than random expectation in Peruvian rainforests (Planque and Slabbekoorn 2008); temporal overlap between species is reduced below chance levels in Costa Rican and Hawaiian communities, with temporal partitioning identified as the primary strategy communities use to manage acoustic competition (Hart et al. 2015); and species more acoustically dissimilar from one another tend to vocalise at the same location and time, consistent with partitioning across both axes (Staniewicz et al. 2023). In Indian grasslands, convergent overdispersion in acoustic signal space emerged independently in two biomes with entirely different species compositions, suggesting that acoustic partitioning is a robust community-level outcome (Lahiri et al. 2021).

When migrants arrive, they add signals to acoustic space already structured by residents. Sblendorio et al. (2024) demonstrated in North America that migrating warblers overlapped the acoustic signal space of resident breeding species for two-thirds of the breeding season, imposing real acoustic costs on residents. Only a few studies in India have empirically tested this. Krishnan (2019) found that during winter migrant influx in a peninsular Indian dry-deciduous habitat, the seasonal turnover in acoustic community composition is visible while overdispersion was broadly maintained. Whether this pattern holds in the structurally and compositionally distinct Himalayan foothill community, with its far larger migratory influx of vocally active Palearctic and elevational passerines, remains unknown. Passive acoustic monitoring with autonomous recorders now makes it feasible to track such seasonal acoustic community dynamics continuously across multiple stations and months (Sugai et al. 2019; Pijanowski et al. 2011), and high-temporal-resolution sampling detects substantially more species diversity than low-resolution approaches (Metcalf et al. 2022).

The Himalayan Foothills: Study System and Knowledge Gaps

The Himalayan foothills of northern India sit at the base of one of the world's most important migratory corridors. Each winter, millions of Palearctic and elevational migrants- warblers, flycatchers, thrushes, and pipits, descend from Central Asian, Himalayan and European breeding grounds into the sal forests,

scrublands, and mixed green spaces of the Dehradun Valley. A defining feature of this system is the compounding of Palearctic influx with downslope elevational migration: index of species richness peaks shift to lower elevations during the cold season as high-elevation residents move downslope (Hu et al. 2025), intensifying competitive pressure in the foothills beyond that caused by long-distance migrants alone. Srinivasan et al. (2018) showed that competition is the dominant structuring force at lower elevations during winter precisely the zone and season studied here.

Foothill studies in Uttarakhand have characterised structural diversity patterns across habitat types and seasons (Kukreti and Bhatt 2014; Bhatt and Joshi 2011; Joshi and Bhatt 2015; Kaushik et al. 2022), and documented seasonal fluctuations attributable to migration but none has linked compositional change to migrant abundance index or examined competitive mechanisms. The gap is threefold. Geographically, no study has conducted a temporally resolved, process-level analysis of avian community dynamics during migratory influx in the Himalayan foothills, despite the Palearctic-Indian flyway carrying a massive annual movement of birds and the Himalayas being identified as a concentration zone for threatened narrow-range migratory species (Somveille et al. 2013; Sanderson et al. 2006). Temporally, existing regional studies compare broad seasonal categories rather than tracking community change month by month across the full migratory cycle, a resolution insufficient to detect niche contraction, dietary shift, or acoustic reorganisation, which operate on timescales of weeks (Guillaumet and Russell 2022). Integratively, no study in this region has simultaneously measured bird community metrics and resource covariates -arthropod abundance index and fruit availability in the same analytical framework, making it impossible to disentangle competition-driven community shifts from those driven by environmental seasonality acting directly on residents.

The present study addresses all three gaps simultaneously, constituting the first multidimensional, temporally resolved, and mechanistically framed investigation of avian community responses to migratory influx in the Western Himalayan foothills. Data were collected monthly from December 2024 through April 2025 at five fixed stations on the Wildlife Institute of India (WII) campus, spanning peak-migrant, and post-migrant periods, with concurrent measurement of insect abundance index at each

station. Three complementary objectives address the community, individual, and acoustic dimensions of the resident response.

Study Objectives and Research Questions

Objective 1: Temporal Dynamics of Avian Community Structure.

This objective quantifies how the arrival and departure of migratory birds influences temporal changes in avian community composition and abundance index at the study site.

Research question: how does migratory influx reshape resident avian community structure in terms of index of species richness and beta diversity across the full migratory cycle in the Himalayan foothills?

Objective 2: Foraging Ecology, Niche Dynamics and Diet Shift of Resident Bulbuls.

This objective examines how the three resident bulbul species (*Pycnonotus cafer, P. jocosus, and P. leucogenys*) adjust their foraging niche and diet in response to migratory influx.

Research questions: in what ways do resident bulbuls adjust their foraging behaviour across height, substrate, microhabitat and manoeuvre during periods of high migratory abundance index? How does this shift when migrant abundance index is controlled against concurrent variation in insect abundance? Is there any diet shift for this resident bulbuls during migratory season and after migratory season?

The central hypothesis is that increased competition for arthropod prey during peak migration will drive niche breadth contraction across foraging dimensions, with expansion following migrant departure, consistent with competitive niche contraction and release (Van Valen 1965; Jedlicka et al. 2006; Kent and Sherry 2020). And for the diet part, during the migratory season, bulbuls are likely to rely more on fruits, possibly due to increased competition with migratory birds for insect prey. After the migrants leave, their diet is expected to include a higher proportion of insects

For this objective 2 behavioural observations focused on three resident bulbul species: the Red-vented Bulbul (*Pycnonotus cafer*), Red-whiskered Bulbul (*Pycnonotus jocosus*), and Himalayan Bulbul (*Pycnonotus leucogenys*), all abundant, year-round residents of the Western Himalayan foothill zone.

All three are omnivorous passerines that forage across multiple strata, consuming fruits, invertebrates, and nectar, and are therefore expected to experience direct competitive overlap with insectivorous Palearctic and elevational migrants during the dry winter months. Their dietary flexibility is precisely what makes them informative focal subjects: because they already exploit a broad range of food types and foraging positions, they can shift their diet by consuming more to fruits rather than insects by avoiding competition with migrants, also there will be a chance of spatial displacement which happens by bulbuls being forced to explore more vertical strata to get their food. Their abundance, conspicuousness, and sedentary territorial behaviour make them tractable subjects for the monthly focal follow sessions on which the foraging analyses of this study depend.

Objective 3: Acoustic Community Structure during Migratory Influx.

This objective examines how the seasonal influx of vocally active Palearctic migrants alters acoustic community structure at the study site.

Research question: is the overdispersion of acoustic signal parameters in the resident community maintained across months despite species turnover driven by migratory influx? The prediction is that overdispersion will be maintained even as species composition changes, consistent with the robust acoustic partitioning documented in other systems (Krishnan 2019; Lahiri et al. 2021), though the degree to which incoming migrants fill or disrupt partitioned signal space will be quantified.

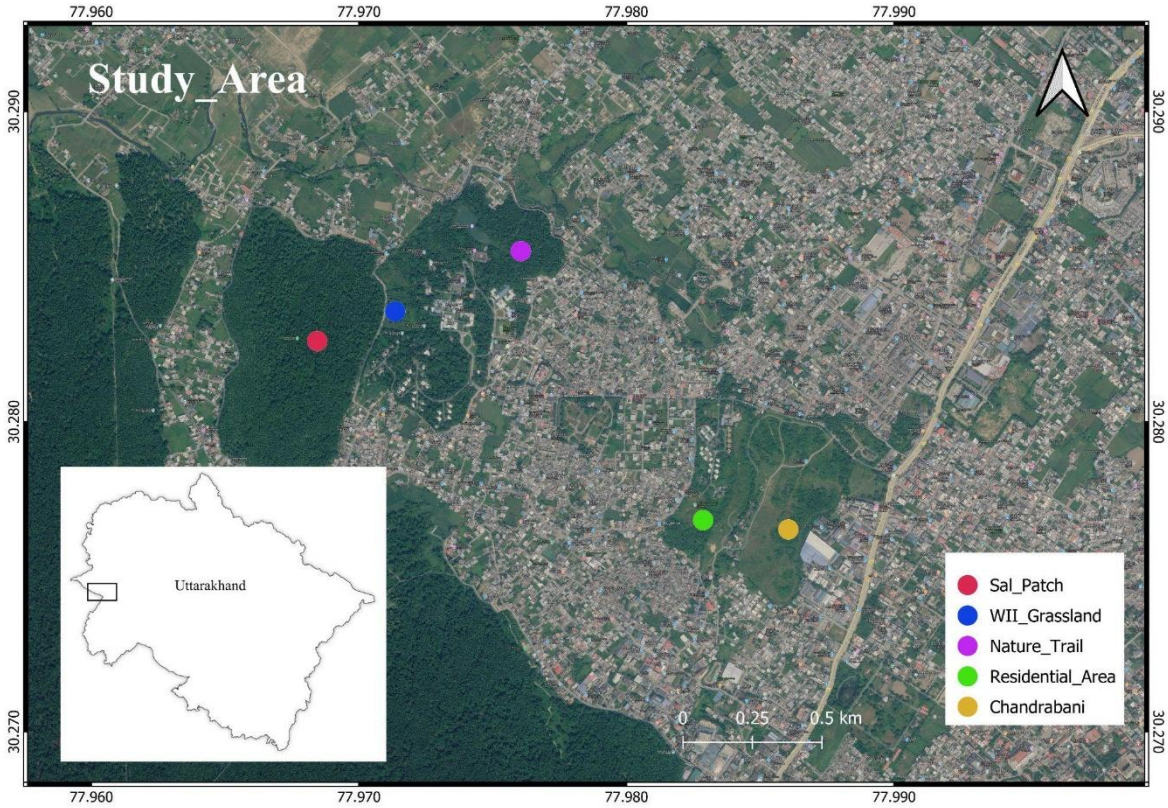
2. STUDY AREA

This study was conducted at the Wildlife Institute of India (WII) campus in Chandrabani, Dehradun, Uttarakhand (77°57'50" to 77°58'45" E; 30°16'40" to 30°17'15" N; 640-665 m asl), situated at the biogeographic interface of the lesser Himalayan foothills and the Indo-Gangetic plains. The campus forms part of the Western Himalayan foothill zone, a region recognised as a critical wintering ground on the Central Asian Flyway and one of the most important avian biodiversity corridors in the Indian subcontinent (Sanderson et al. 2006). The site encompasses approximately 80 acres of structurally heterogeneous habitat, including secondary Sal (*Shorea robusta*) forest at various successional stages, natural scrub, streamside vegetation, and managed green space, embedded within a peri-urban landscape adjacent to Rajaji National Park.

The climate is humid subtropical with a pronounced dry winter (December-February, temperatures occasionally reaching 5°C at night) that coincides precisely with peak Palearctic and elevational migrant presence, the period of ecological resource scarcity that forms the core temporal context of this study.

The WII campus supports exceptional avian diversity, recorded as the most avian-rich academic institution in India, with 206 species documented during the 2026 Campus Bird Count (birdcount.in/cbc26-final-results/), and a cumulative hotspot list exceeding 373 species (eBird hotspot L2348198). This assemblage comprises a year-round community of resident Himalayan foothill species alongside a substantial seasonal influx of Palearctic and Elevational winter migrants, warblers, flycatchers, thrushes etc., arriving in October-November and departing by March-April. This dramatic seasonal pulse of vocally active, ecologically similar migrants into an already species-rich resident community makes the campus an ideal site for studying multi-dimensional niche responses across temporal, trophic, and acoustic axes. The study area map is shown in Figure 1.

Figure 1. Study area Map marked by five study sites in and around WII Campus



3.METHODOLOGY

3.1.Field Methods

3.1.1.Objective 1

Point counts were conducted at five sites once per week, during which all bird species detected visually or acoustically within a 15-minute period were recorded and for this 15 minutes repeated counting of individuals has avoided. Surveys were carried out between 09:00-09:15 h during winter and 08:30-08:45 h during summer. Bird species that could not be confidently identified in the field were photographed and subsequently identified using the field guide *Birds of the Indian Subcontinent*. Vocalizations were recorded and identified with the aid of the mobile application Merlin Bird ID. Data were collected over a five-month period, resulting in a total of 89 survey visits.

3.1.2. Objective 2

Focal animal sampling (Altmann 1974) was used to record foraging behaviour of three resident Bulbul species: Himalayan Bulbul (*Pycnonotus leucogenys*), Red-vented Bulbul (*Pycnonotus cafer*), and Red-whiskered Bulbul (*Pycnonotus jocosus*), across five study sites immediately following point count surveys. Focal follows were conducted on solitary individuals to avoid pseudoreplication and group bias, with each follow lasting approximately five minutes or until the individual was lost from view.

Foraging bouts were recorded continuously throughout each focal follow, to assure the independence of observation, only initial observation is taken for further analysis. For each bout, the following behavioural and spatial variables were recorded: vertical stratum used (ground level: 0 m; shrub layer: 0-4 m; sub-canopy: 4.1-8 m; canopy: 8-12 m; top canopy: >12 m), foraging manoeuvre (**Gleaning**-Picking prey directly off a surface (leaf, bark, branch, ground) while perched or moving slowly; no flight involved.**Pecking**-Forceful bill strike against a substrate to dislodge or extract prey; distinguished from gleaning by the striking action rather than a simple pick-up, **Sallying**-Flying out from a perch to capture prey (in air or off a surface) and returning to a perch, **Reaching**-Stretching neck or bill toward prey without repositioning the feet; body stays stationary, **Hanging**-Clinging in an inverted or tilted posture to access the underside of leaves, branches, or fruit clusters, **Hovering**-Stationary flight

maintained by rapid wingbeats while taking prey, without launching from or returning to a perch(Remsen and Robinson 1990), and substrate type (fruit, flower, leaf, air, ground, bark/branch). Data were collected in the Epicollect App and transcribed daily into standardised spreadsheets, yielding a target of 15 bouts per species per week.

For insect sampling, five sets of pan traps, each consisting of one yellow, one white, and one blue trap, were placed on the ground at five different sites. Sampling was repeated every week. The collected insects were dried, and their biomass was measured using a weighing balance with a precision of 0.01 g. Pan traps are a simple, low-cost, and standardized method for collecting flying insects, particularly pollinators and other flower-visiting insects. They can capture a large number of insects with relatively little field effort. However, they do not represent the entire insect community, as they are more effective at catching certain groups of flying insects than others.

For blood sample collection, twelve-meter nylon mist nets with 36 mm mesh size were set up at fixed stations. Nets were deployed weekly for 2-3 hours, primarily within three hours after sunrise. Nets were monitored continuously to ensure that birds were safely extracted within 5 minutes to minimize stress. All captured birds were released immediately at the capture site after processing. Each bird was fitted with a uniquely numbered aluminum leg ring to prevent resampling and to allow individual identification in future sessions (Johnston et al. 1997). Standard measurements including species identification, weight, wing length, and tarsus length were recorded, and the bird's health condition was assessed before release. A small quantity of blood sample (~10 µl) was collected from the brachial vein using a disposable syringe-needle of 27-30 gauge and stored in 1.5 ml Eppendorf vials without any solvent. All samples were refrigerated until further processing.

Sample preparation and Isotope analysis

Blood samples were dried in a hot air oven at 56 °C. Dried blood was scraped from the vial using a sterile spatula. Because only a small volume of blood (~10 µL) was collected, whole blood was analysed rather than separating plasma and red blood cells. Samples were placed in tin capsules with sample mass (0.3–0.8 mg) adjusted to produce a peak of 3–8 nA in a mass spectrometer. Carbon and nitrogen isotope ratios were measured simultaneously by continuous-flow isotope ratio mass spectrometry (EA-

IRMS) using a Vario Pyro cube elemental analyser (Elementar, Langenselbold, Germany) attached to an Isoprime 100 isotope ratio mass spectrometer (Elementar, Manchester, UK) at the IRMS facility, Indian Institute of Science Education and Research Pune. Stable isotope ratios are expressed in delta (δ) notation in ‰ (per mil or parts per thousand) according to the formula:

$$\left[\frac{(R_{sample} - R_{standard})}{R_{standard}}\right] \times 1000 = \delta$$

where,

R_{sample} = ratio of the heavy isotope to light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) in the sample;

$R_{standard}$ = ratio of the heavy isotope to light isotope in standard, V-PDB (Vienna - Pee Dee Belemnite) for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

The repeatability was assessed by analysing laboratory standards – Sulphanilamide ($\delta^{13}C$ = -27.8‰, $\delta^{15}N$ = -6.3‰), MERC ($\delta^{13}C$ = -12.1‰), FLUCA ($\delta^{13}C$ = -26.7‰) and ammonium sulphate (USGS25) ($\delta^{15}N$ = -30.4‰) reference materials.

3.1.3. Objective 3

Audiomoths were deployed at the five study sites for five days per month from December to May. Data for March were not obtained because of a technical failure in the AudioMoth. Time was set from 7:00-10:00 h and 14:00-17:00 h in winter and 6:00 -9:00 h and 15:00-18:00 h in summer. Audiomoth configured with a sample rate of 48 kHz, Medium Gain, Sleep duration 2:00 minute and recording duration 2:00 minute. Each day produced 90 files; however, due to defects in the AudioMoth, some files did not contain any recordings. Due to time constraints data from only one audiomoth was analyzed.

3.2. Analytical Methods

3.2.1. Objective 1

Data Preparation and Derived Metrics

To characterise the avian community at each sampling occasion, two primary response variables were derived from the raw point count data: index of species richness, calculated as the number of species recording at least one individual per site visit, and total abundance index index, calculated as the sum of all individuals recorded across all species per site visit. This has done separately for migrants and residents. This assessment of migrants and residents in the study area is assessed using bar charts in eBird for the specific region. These metrics were subsequently averaged across all stations within each month to generate monthly study-area means, enabling temporal comparisons across the December-April study window.

Temporal Patterns in Index of species richness and Abundance index

Monthly variation in index of species richness and index of abundance was first summarized descriptively using means, standard errors, medians, and ranges for each month. To account for repeated sampling across survey sites and potential site-level heterogeneity, generalized linear mixed models (GLMMs) were used to evaluate temporal variation in community metrics. Month was included as a fixed effect, while Site was included as a random intercept to account for non-independence among repeated observations from the same site.

Index of species richness and total abundance index were analysed using negative binomial GLMMs implemented in the package glmmTMB. The negative binomial distribution was selected because both response variables were count data and exhibited overdispersion relative to a Poisson distribution. The significance of monthly variation was assessed using Type II Wald chi-square tests. To evaluate whether inclusion of Month improved model fit, each full model was compared with a corresponding null model containing only the random effect of Site using likelihood-ratio tests.

Multivariate Community Composition Analysis

To quantify compositional dissimilarity between each pairwise site visits, a Bray-Curtis dissimilarity matrix was constructed from species abundance index data using the *vegan* package in R . The Bray-Curtis index was selected because it is sensitive to species abundance index rather than mere presence or absence, it is unaffected by joint absences, which are uninformative in species-rich systems where most species are absent from any given site visit, and it has been extensively validated for avian community analyses.Temporal patterns in community composition were visualised using Non-metric Multidimensional Scaling (NMDS), an unconstrained ordination technique that represents the rank-order dissimilarities between sampling units in reduced dimensional space (Clarke, 1993).To test statistically whether avian community composition differed significantly across months and seasons, Permutational Multivariate Analysis of Variance (PERMANOVA) was applied to the Bray-Curtis dissimilarity matrix using the adonis2 function in vegan. PERMANOVA partitions multivariate dissimilarity into within-group and between-group components and assesses significance through permutation, making no assumptions about multivariate normality, an important consideration given the structure of species abundance index data .Because PERMANOVA is sensitive to both differences in group centroids (true compositional differences) and differences in within-group dispersion (variability), permutational analysis of multivariate dispersion (PERMDISP) was conducted alongside each PERMANOVA model using the *betadisper* function in *vegan*. PERMDISP tests whether the average distance of sampling units to their group centroid differs across groups. Non-significant PERMDISP results ($p > 0.05$) confirm homogeneous within-group dispersion, validating that significant PERMANOVA results can be attributed to genuine differences in community composition rather than artefacts of unequal spread.To determine the mechanistic basis of temporal community turnover specifically whether compositional change across months was driven by species replacement or by the loss and gain of species from a shared species pool beta diversity was partitioned into its turnover and nestedness components following the framework of Baselga (2010).

All analyses were conducted in R (version 4.6). Key packages used were: vegan (multivariate community analysis), betapart (beta diversity partitioning) and ggplot2 (visualisation).

3.2.2. Objective 2

Niche Breadth Calculation

Foraging niche breadth was quantified using Levins' index (Levins 1968), standardised to a 0-1 scale following Hurlbert (1978), separately for four foraging dimensions: vertical stratum use, microhabitat, foraging manoeuvre, and substrate use. The standardised Levins' index (B') was calculated as:

$Bs = (B - 1) / (n - 1)$

where $B = 1 / \Sigma p^2_i$ is the raw Levins' index, p_i is the proportion of foraging bouts recorded in category i, and n is the total number of categories within each dimension (vertical strata: n = 5; foraging manoeuvre: n = 5; substrate: n = 6; microhabitat: n = 3). A value of 0 indicates complete specialisation on a single category, while a value of 1 indicates equal use of all categories.

To increase the stability of niche breadth estimates, foraging bouts were pooled into bi-weekly temporal blocks (Bi-week 1 = Weeks 1-2, Bi-week 2 = Weeks 3-4, and so forth), resulting in 10 bi-weekly data points per species across the December–April study period. All calculations were performed in R version 4.6 using the tidyverse package.

Linear mixed-effects model with logit transformation of Y

To assess the effect of migratory bird index of species richness and insect biomass on foraging niche breadth, linear mixed-effects models were fitted. Standardised Levins' B' was used as the response variable for each of four foraging dimensions: vertical strata, microhabitat, substrate, and maneuver. Prior to analysis, B' values were logit-transformed; log(p/1-p) to satisfy the assumption of an unbounded continuous response, following boundary adjustment using y = (y(n-1) + 0.5)/n to handle values at or near 0 and 1 (Smithson & Verkuilen 2006). All 30 observations (10 bi-weeks × 3 species) were included in a single model per foraging dimension. Response variables were migrant species richness index (mean number of migratory species detected per bi-week) and insect biomass (mean bi-weekly biomass from pantrapping). A null model containing only species(Red-vented Bulbul, Red-whiskered Bulbul, Himalayan Bulbul) as the random intercept was compared to the full model using AIC and likelihood ratio tests.

Visualization of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio from blood

Red blood cells provide a short-term dietary integration window of 2-4 weeks.. The isotopic niche width of species quantified using sample-size corrected 95% Bayesian standard ellipse areas (SEAc) employing functions available in the R package 'siber' (version 2.1.6).

3.2.3.Objective 3

Species Activity and Species Turnover

Raven Pro 1.6 was used to visualize spectrograms, along with the BirdNET V2.4 machine learning detector to identify birds. . BirdNET V2.4 was set to a threshold of 0.25 for quality detections and identification. And suppressed the species which is not present in WII manually. All 2-minute recordings were then examined, and all species calling in each recording were identified. A species-recording absence-presence matrix was created, where 1 indicated the presence of a species in a recording and 0 indicated its absence. The matrix also included columns for month and day.

To focus the analysis on regularly occurring species and avoid bias from species that were only occasionally detected, only species that were present in 5% or more of the total recordings within each month were retained. This proportional threshold was applied separately for each month, following the approach of Luther (2009) and Krishnan (2019). The reduced threshold of 5%, compared to the 10% used in those studies, was chosen to account for the shorter recording duration of 2 minutes per clip, which reduces the probability of detecting a species in any single recording compared to the 45-minute sessions used in previous work. Species meeting this criterion in a given month are hereafter referred to as the acoustic community of that month.

For each species within the acoustic community, an acoustic abundance index index was calculated following Krishnan (2019). To ensure that each recording day contributed equally to the index regardless of how many recordings were made on that day, 4 recordings were randomly drawn from each of the 5 sampling days within a month, giving a total of 20 recordings per draw. For each draw, the proportion of recordings in which the species was detected was calculated. This process was

repeated 1000 times, and the mean proportion across all iterations was taken as the acoustic abundance index index for that species in that month. The index ranges from 0 to 1, where a value close to 1 indicates a species that is reliably detected across recordings, and a value close to 0 indicates a species that is rarely detected. This bootstrapped approach accounts for day-to-day variation in vocal activity and avoids bias from days with unusually high or low recording effort. To calculate species turnover and diversity accounting for abundance index, Jaccard similarity indices were calculated between the five monthly communities, and Shannon–Wiener alpha-diversity indices were calculated for each month using the vegan package in R.

Acoustic Community Structure and Space

To examine how acoustic community structure shifts across months, 6 acoustic parameters (Peak Frequency Contour Max Frequency (Hz), Peak Frequency Contour Min Frequency(Hz), Peak Frequency(Hz), Bandwidth 90%(Hz),Peak Time Relative, Duration 90%(s))were extracted for all identified species from every recording using Raven Pro 1.6 and categorized into different months according to the species present in each month. PCA was performed on these variables to reduce dimensionality, and MANOVA was conducted on the resulting principal components. A Kolmogorov–Smirnov test was also performed to determine whether overdispersion was present in monthly communities. The assumption was that if a community is overdispersed, it would violate normality and be statistically indistinguishable from 100 random uniform distributions (Krishnan 2019).

To assess similarity in acoustic community structure between seasons, December, January and February joined to create a winter community and April and May joined to create a summer community. And using this the mean nearest-neighbour distance (NND) was calculated between species in the winter community and their closest species in the summer community using the first three principal components. A null model approach was then used by generating 10,000 randomized communities of the same size as the summer community and spanning the same range of values in acoustic space. Mean NND was calculated for each randomized community to generate a null distribution. The observed NND was compared with this null distribution using a Z-score. Significantly lower observed NND

values than expected by chance were interpreted as evidence that winter and summer communities occupied similar regions of acoustic space despite differences in species composition.

4. RESULTS

4.1. Objective 1

Temporal Patterns of Index of species richness and Abundance index

A total of 155 bird species were recorded across 89 site visits spanning December to April at five habitat sites in the Himalayan foothills. Species richness Index per site visit ranged from 2 to 55 species, and total abundance index ranged from 8 to 315 individuals across the study period. Summary of the richness and richness across month is given in Table 1 and Table 2 respectively and graphically in Figure 2 (a) and (b)

Table 1. Variation of index of species richness across months. Data is presented as the mean of the five study sites.

Month	n	mean	sd	se	median	min	max
Dec	23	18.6	6.56	1.37	19	7	31
Jan	18	19.4	10.2	2.41	18	9	54
Feb	16	20.9	13.1	3.28	17.5	1	51
Mar	15	17.8	7.67	1.98	16	8	32
Apr	17	15.2	5.56	1.35	15	5	23

Table 2.Variation of mean abundance index across months. Data is presented as the mean of the five study sites.

Month	n	mean	sd	se	median	min	max
Dec	23	58.5	30.5	6.36	49	17	119
January	18	67.8	51.2	12.1	60	21	253
February	16	83.3	73.3	18.3	69.5	6	313
March	15	63.5	37.2	9.6	56	12	144
April	17	39.7	22.3	5.42	38	5	88

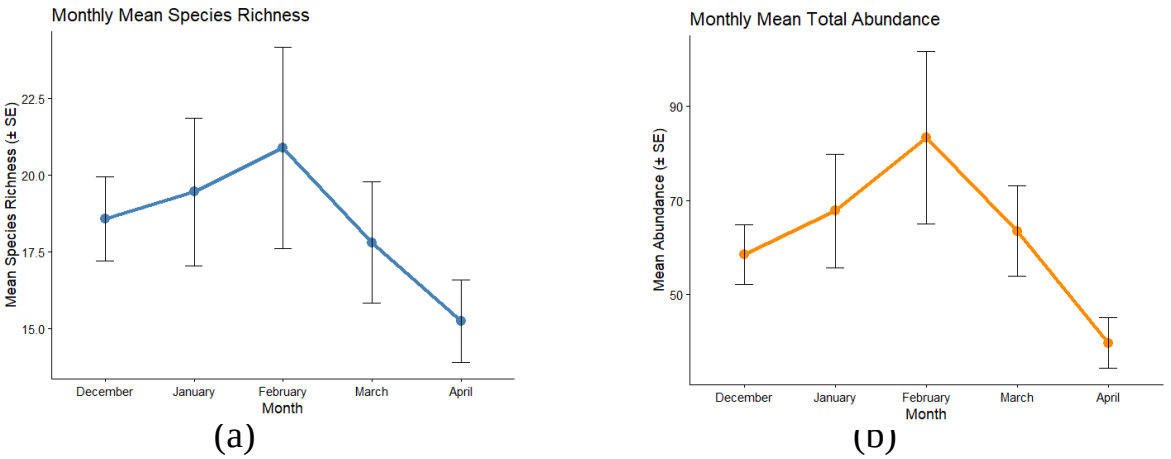


Figure 2. (a) Mean Total monthly richness index unimodal pattern (b) Mean Total abundance index pattern across months

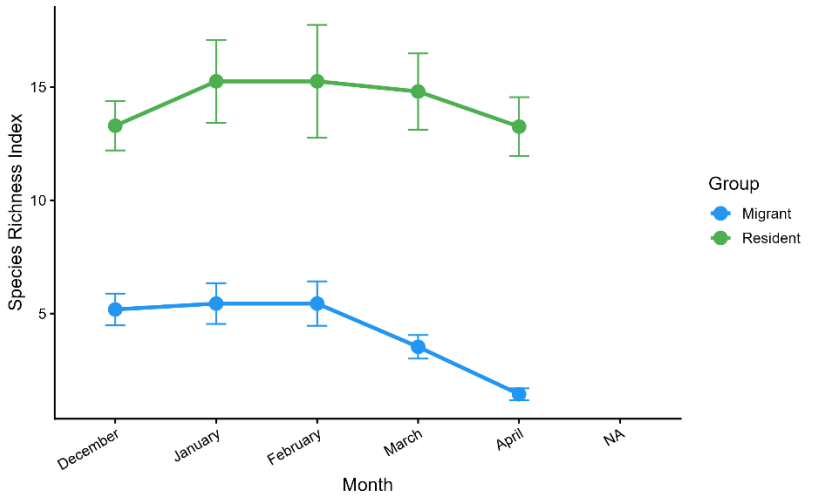


Figure 3. Species richness Index across month; Migrants vs Residents

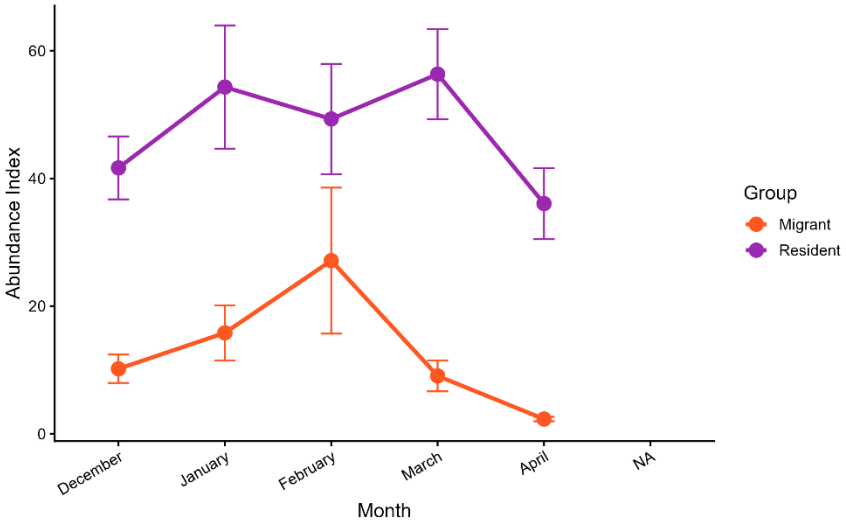


Figure 4.Species abundance Index across month; Migrants vs Residents

When pattern analysed separately for migrants and Residents; Species richness Index and abundance Index followed markedly different seasonal trajectories for migrants and residents (Figure 3 and 4). Resident bird richness and abundance remained comparatively high and stable across all months (December–April), consistent with their year-round occupancy of the study area. In contrast, migrant richness and abundance were lower overall and declined sharply from March onward, reaching their lowest values in April. This pattern is consistent with the expected phenology of Palearctic migrants, which typically arrive in the region in early winter, remain through the peak wintering months (December–February), and then depart northward toward their breeding grounds as spring approaches explaining the near-absence of migrants recorded by late April.

Monthly variation in index of species richness and total abundance index was analysed using negative-binomial generalized linear mixed models (GLMMs), with Month included as a fixed effect and Site as a random effect to account for repeated sampling across survey locations. Model diagnostics indicated no evidence of overdispersion or zero inflation for either richness or abundance index, suggesting an adequate model fit.

Index of species richness did not vary significantly among months after accounting for site-level variation (likelihood-ratio test: $\chi^2 = 4.50$, df = 4, p = 0.342). Although richness tended to be higher in February relative to April, the overall effect of Month was not significant (Type II Wald $\chi^2 = 4.67$, df = 4, p = 0.323).

In contrast, total abundance index showed significant monthly variation after accounting for site-level variation (likelihood-ratio test: $\chi^2 = 11.81$, df = 4, p = 0.019). The overall effect of Month was significant (Type II Wald $\chi^2 = 12.95$, df = 4, p = 0.012), with abundance index being higher in December, January, February and March compared to April. The strongest increase in abundance index was observed in February.

Multivariate Community Composition Analysis

NMDS ordination of Bray-Curtis dissimilarities among all 89 site visits revealed structured temporal variation in avian community composition across the study period. The initial two-dimensional solution yielded a stress value of 0.26, exceeding the acceptable threshold of 0.20 (Clarke, 1993), and was therefore considered an unreliable representation of compositional distances. A three-dimensional NMDS solution reduced stress to 0.187, falling within the acceptable range, and was used for all subsequent visualisation and interpretation. NMDS ordination revealed considerable overlap in community composition across all five months, with no clearly distinct monthly clusters evident in either ordination projection (Figure 5). All monthly groups occupied largely shared ordination space, indicating broadly similar community composition throughout the study period. However, a degree of separation was apparent along NMDS axis 1 in both projections, with December and January visits tending toward negative axis 1 values and March and April visits distributed more broadly, suggesting a gradual compositional shift across the season. February visits showed the widest spread in ordination space, consistent with the high within-month variability reflected in its large standard error for both richness and abundance index.

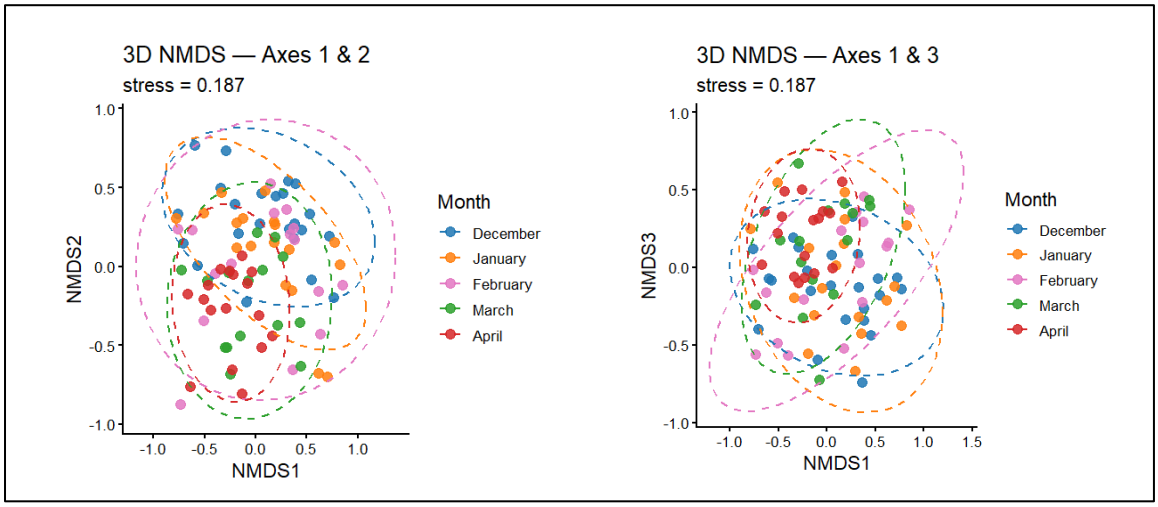


Figure 5. Three-dimensional NMDS ordination of avian community composition across months based on Bray-Curtis dissimilarity (stress = 0.187). The left panel shows axes 1 and 2; the right panel shows axes 1 and 3.

A PERMANOVA based on Bray–Curtis dissimilarities revealed significant effects of both site and month on bird community composition. Site identity explained 25.7% of the variation in community structure ($R^2 = 0.257$, $F = 7.69$, $p = 0.001$), whereas month explained 7.6% of the variation ($R^2 = 0.076$, $F = 2.29$, $p = 0.001$). The larger effect size for the site indicates that spatial variation in community composition was stronger than temporal variation across months. (Table 3)

Table 3. PERMANOVA results testing the independent effects of month and site on avian community composition (Bray-Curtis dissimilarity; 999 permutations).

Source of variation	**df**	**Sum of Sqs**	**R2**	**F**	**P value**
Site	4	7.664	0.25654	7.6908	0.001
Month	4	2.2799	0.07632	2.2878	0.001
Residual	80	19.9305	0.66714		
Total	88	29.8744	1		

To verify that PERMANOVA results were not driven by differences in multivariate dispersion, a PERMDISP analysis was conducted. Dispersion did not differ significantly among months ($F = 1.01$, $p = 0.423$), indicating that the observed monthly differences reflected shifts in community composition rather than unequal within-month variability. This confirms that the significant PERMANOVA results reflect genuine differences in community composition among temporal groups rather than artefacts of unequal within-group variability (Anderson, 2006).

Pairwise Sørensen beta diversity between monthly communities ranged from 0.194 (January vs February) to 0.451 (December vs April), with a mean total beta diversity of 0.314 across all month pairs . Of this total compositional dissimilarity, 70.4% was attributable to species turnover (mean β~sim~ = 0.221) and 29.6% to nestedness (mean β~sne~ = 0.093), indicating that temporal community change across the study period was driven predominantly by species replacement rather than by the loss or gain of species from a shared pool (Figure 6).

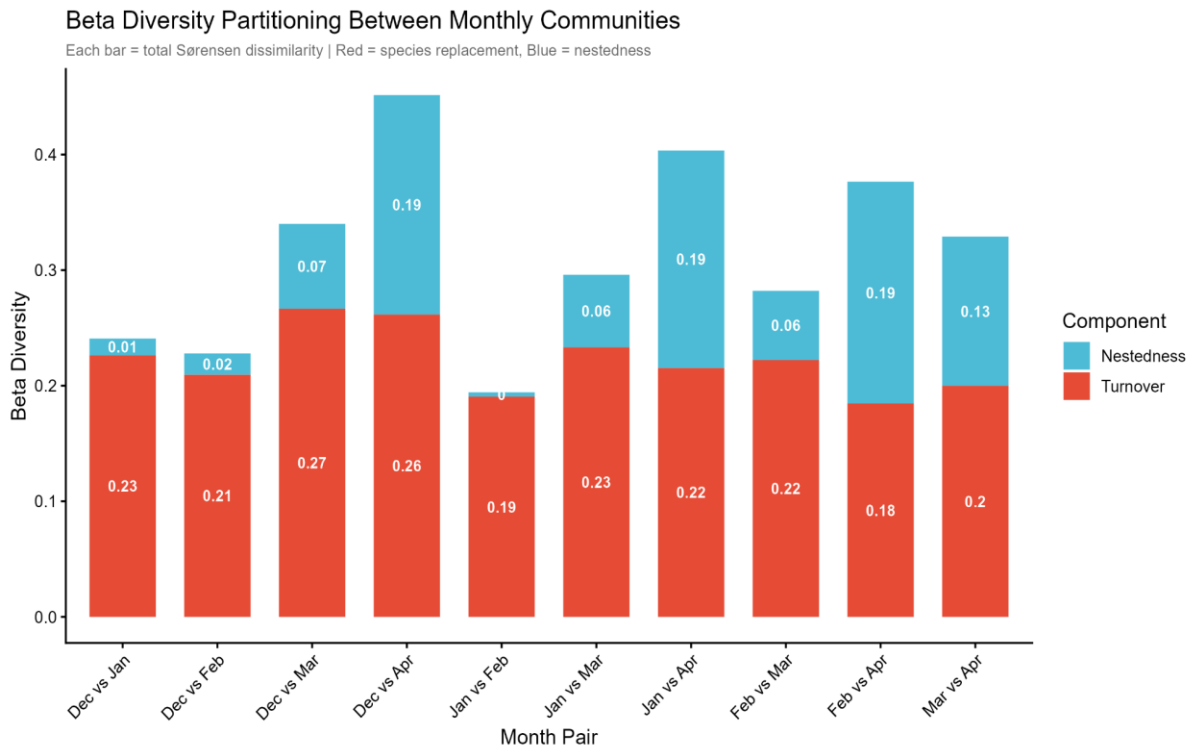


Figure 6. Beta diversity partitioning between monthly avian communities based on Sørensen dissimilarity. Each bar represents total pairwise dissimilarity between two monthly communities, partitioned into species turnover (red) and nestedness (blue). Values within bars indicate the magnitude of each component.

4.2.Objective 2

Foraging effort and prey use

A total of 919 independent foraging bouts were recorded across the three resident bulbul species over the study period (December-April): 319 bouts for Himalayan Bulbul (HB), 312 for Red-vented Bulbul (RVB), and 288 for Red-whiskered Bulbul (RWB). Foraging bouts were distributed across 10 biweekly periods, ranging from 25 to 42 bouts per bi-week (BW) per species. Fruit was the dominant prey type across all three species throughout the study period, accounting for 68% of HB bouts, 71% of RVB bouts, and 72% of RWB bouts (Figure 7). Insect consumption was highest during December and January across all species and declined substantially by March and April. Flower foraging, in contrast, increased from near absence in December to a notable proportion of bouts by February-March, coinciding with the onset of flowering phenology at the study site.

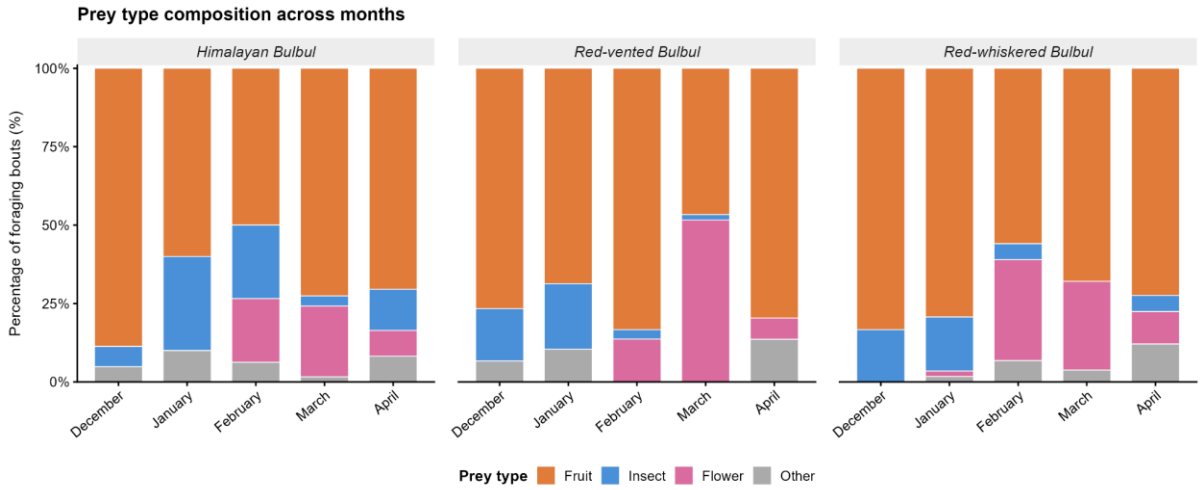
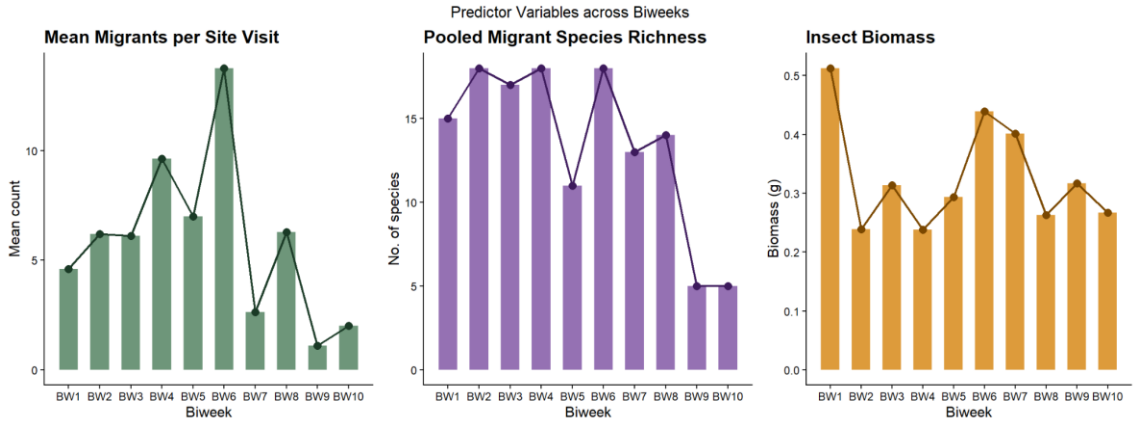


Figure 7. Prey type composition of foraging bouts across months for three resident bulbul species - Himalayan Bulbul, Red-vented Bulbul, and Red-whiskered Bulbul. Bars represent the percentage of foraging bouts allocated to each prey type (fruit, insect, flower, and other) per month.

Temporal variation in migratory abundance index and insect biomass

Migratory bird abundance index showed clear temporal variation across the study period. Mean migrants per site visit ranged from 1.11 (BW9, late March) to 13.75 (BW6, mid-February) (Figure 8a), with an overall mean of 5.93 ± 3.76 migrants per site visit. Migratory richness was high during most months and declined sharply BW8 onwards as migrants departed (Figure 8b).

Insect biomass also varied across bi-weeks, ranging from 0.238 g (BW4) to 0.513 g (BW1), with an overall mean of 0.328 ± 0.093 g. Insect biomass was relatively higher at the beginning of the study period (December, BW1) and did not show a strong directional trend across bi-weeks (Figure 8c).



(a) (b) (c)

Figure 8.(a). Mean migrant abundance index per site visit across ten biweekly sampling periods.(b). Pooled migrant index of species richness across ten biweekly sampling periods.(c). Mean insect biomass (g) across ten biweekly sampling periods.

Temporal variation in foraging niche breadth

Standardised Levins' B' was calculated for four foraging dimensions, vertical strata, microhabitat, substrate, and maneuver, per species per bi-week. Descriptive graphs are presented in Figure 9.

Across all three species, substrate niche breadth showed the narrowest values overall (HB: 0.411 ± 0.167; RVB: 0.409 ± 0.188; RWB: 0.419 ± 0.225), indicating that all three species were relatively specialised in their substrate use regardless of season. Maneuver niche breadth was consistently broader, suggesting greater flexibility in foraging technique.

Temporal trends in B' differed across species and dimensions. In HB, vertical niche breadth showed a declining trend from BW1 (B' = 0.650) to BW10 (B' = 0.305), suggesting a progressive narrowing of vertical space use across the study period. RVB showed higher overall niche breadth values in vertical strata and microhabitat during mid-study bi-weeks (BW5-BW7), coinciding with the peak and immediate post-peak migration period. RWB showed relatively stable maneuver niche breadth across bi-weeks (range: 0.369-0.735, mean = 0.594 ± 0.104), while vertical and microhabitat niche breadth were more variable.

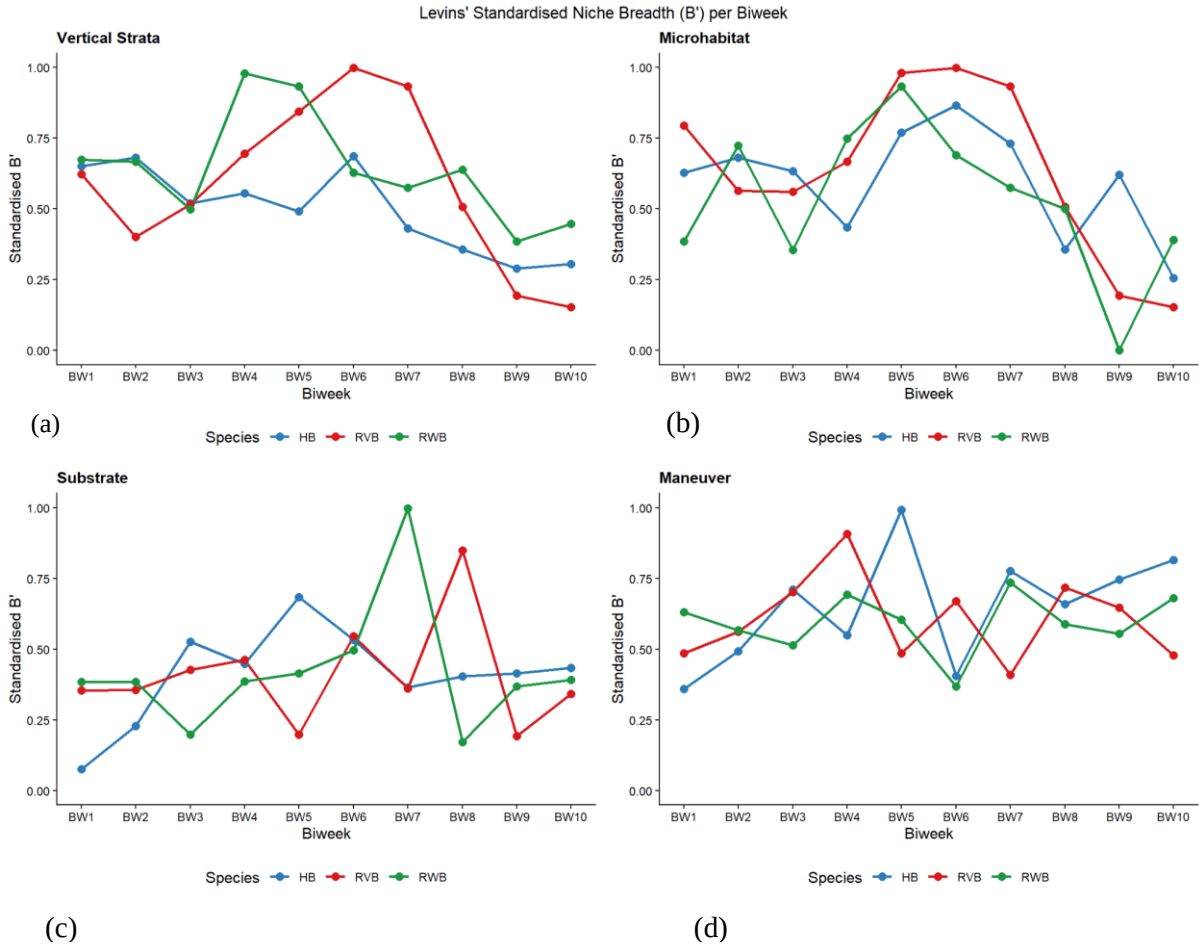


Figure 9.(a). Levins' standardised niche breadth (B') for vertical stratum use across ten biweekly sampling periods for three resident bulbul species (HB = Himalayan Bulbul, RVB = Red-vented Bulbul, RWB = Red-whiskered Bulbul).(b). Levins' standardised niche breadth (B') for microhabitat use across ten biweekly sampling periods for three resident bulbul species.(c). Levins' standardised niche breadth (B') for foraging substrate use across ten biweekly sampling periods for three resident bulbul species.(d). Levins' standardised niche breadth (B') for foraging manoeuvre use across ten biweekly sampling periods for three resident bulbul species

Relationship between niche breadth and predictor variables

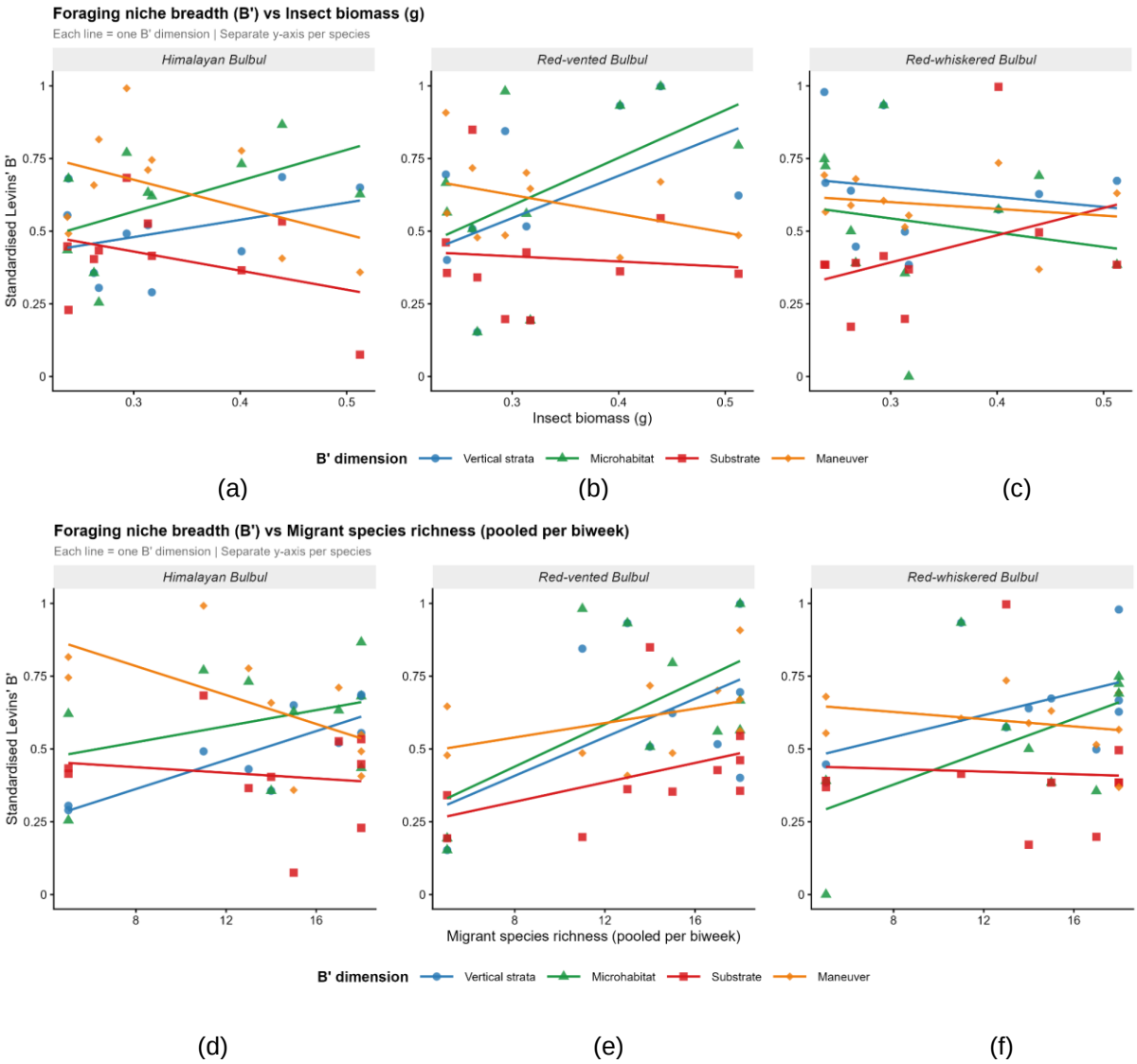


Figure 10. Relationships between standardized Levins' niche breadth (B') and predictor variables for three bulbul species. Panels (a-c) show the association between insect biomass and niche breadth dimensions, whereas panels (d-f) show the association between migrant index of species richness and niche breadth dimensions. Blue, green, red and orange lines represent vertical strata, microhabitat, substrate and manoeuvre niche breadth, respectively.

Figure 10 illustrates the relationships between standardized Levins' niche breadth (B′) and the predictor variables, insect biomass and migrant index of species richness, for the three bulbul species. Correlation patterns differed among niche dimensions and species. Vertical strata and microhabitat niche breadth appeared to show stronger associations with migrant index of species richness, whereas substrate and manoeuvre niche breadth exhibited comparatively weak relationships. Associations with insect biomass were inconsistent across species and niche dimensions.

Linear modeling of niche breath and predictor variables

Table 4. Model Selection Results and Predictor Effects for Vertical, Microhabitat, Substrate, and Maneuver Dimensions

B' dimension	Delta AIC (full vs null)(absolute)	Migrant richness (estimate)	t	Insect biomass (estimate)	t.1
Vertical	6.863	0.105	3.04	1.649	0.884
Microhabitat	5.447	0.112	2.636	2.668	1.161
Substrate	3.895	0.011	0.289	0.057	0.029
Maneuver	0.188	-0.02	-0.757	-2.391	-1.667

Vertical strata. The full model outperformed the null model (ΔAIC = 6.86; LRT p = 0.004). Migrant richness was a significant positive predictor of vertical niche breadth (estimate = 0.105, p = 0.005), indicating that bulbuls used a broader vertical range during periods with more migrant species. Insect biomass and species identity were not significant predictors. The model explained a moderate proportion of variation (adjusted $R^2 = 0.255$).

Microhabitat. The full model also performed better than the null model (ΔAIC = 5.45; LRT p = 0.009). Migrant richness had a significant positive effect on microhabitat niche breadth (estimate = 0.112, p = 0.014), while insect biomass and species identity were not significant. Model explanatory power was moderate (adjusted $R^2 = 0.196$).

Substrate. The null model was better supported than the full model (ΔAIC = 3.90), and the model was not significant (LRT p = 0.949). Neither migrant richness, insect biomass, nor species identity influenced substrate niche breadth. The model explained virtually no variation (adjusted $R^2 = -0.149$).

Maneuver. The full and null models were essentially equivalent (ΔAIC = 0.19; LRT p = 0.123). Neither migrant richness nor insect biomass significantly affected maneuver niche breadth, and explanatory power was low (adjusted $R^2 = 0.034$).

A summary of model support (ΔAIC) and parameter estimates for migrant richness and insect biomass across the four niche dimensions is presented in Table 4.

Stable Isotope Analysis of Dietary Niche During the Non-Breeding Period

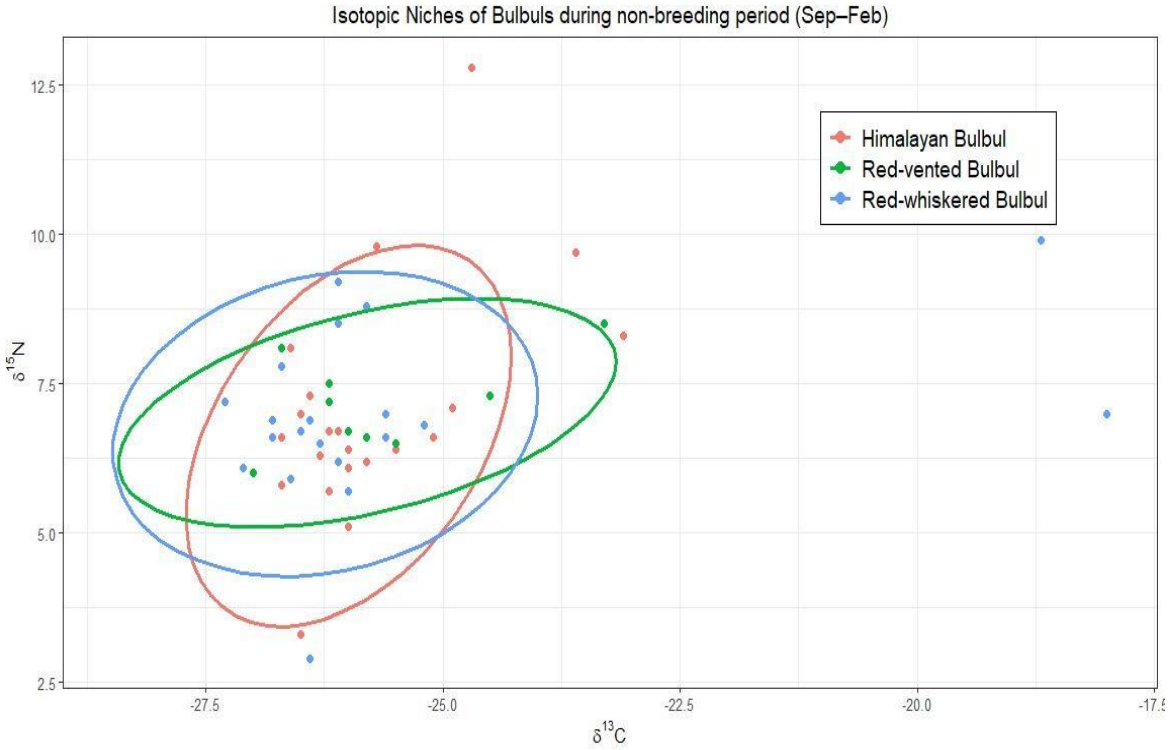


Figure 11. Isotopic niches of three resident bulbul species during the non-breeding period (September–February), plotted as δ¹³C (x-axis) and δ¹⁵N (y-axis). Ellipses represent the standard ellipse area (SEA) for each species, enclosing approximately 40% of the data and indicating the core isotopic niche space. Points represent individual blood samples.

Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) was conducted on blood samples collected from the three resident bulbul species during the non-breeding period (September-February) to characterise their isotopic niche space. Isotopic niches of the three species are presented as standard ellipses in bivariate isotope space (Figure 11).

All three species occupied broadly overlapping regions of isotope space, with $\delta^{13}C$ values ranging approximately from -28 to -22 ‰ and $\delta^{15}N$ values ranging approximately from 3 to 10 ‰ across species. The core isotopic niches of Himalayan Bulbul and Red-vented Bulbul showed considerable overlap, while the Red-whiskered Bulbul ellipse was positioned slightly toward more negative $\delta^{13}C$ values, suggesting marginally greater reliance on C3 plant-based resources during the non-breeding period.

Several outlier individuals were visible outside the standard ellipses in all three species, indicating individual-level dietary variation.

Blood samples collected during the summer (breeding) season could not be processed for isotopic analysis due to delays in sourcing the required reagents and chemicals. As a result, a direct comparison of isotopic niche between the non-breeding and breeding seasons -which was originally planned to test whether bulbuls shift their diet between peak migration and post-migration periods was not possible within the scope of this study. This comparison remains an important objective for future work, as seasonal isotopic shifts would provide an independent, time-integrated measure of dietary change complementing the foraging observation data reported in Objective 2.

4.3.Objective 3

A total of 2,139 two-minute acoustic recordings were collected over five months, with recordings obtained on five sampling days per month. The monthly distribution of recording effort is presented in Table 5. From these recordings, 71 bird species were identified. The number of individuals recorded and the number of species retained after applying the 5% occurrence filter for each month are presented in Table 6.

Table 5. Number of Two-Minute Acoustic Recordings Obtained Across Sampling Months

	No of Recordings				
Month	Day 1	Day 2	Day 3	Day 4	Day 5
April	110	112	112	106	105
December	87	48	75	89	90
February	50	50	50	50	55
January	66	90	88	90	91
May	105	105	105	105	105

Table 6. Total Bird Species Recorded and Number of Species Retained After the 5% Occurrence Filter Across Sampling Months

Month	**Raw Richness**	**Species passed 5%filter**
December	57	19
January	57	19
February	45	17
April	52	21
May	49	23

A total of 32 species met the 5% occurrence threshold in at least one month and were retained for acoustic community analyses (Figure 12). The acoustic abundance index index varied considerably among species and months, indicating temporal changes in community composition. Rose-ringed Parakeet consistently exhibited the highest acoustic abundance index across the study period, while Himalayan Bulbul, Plum-headed Parakeet, Asian Koel, and Ashy Prinia also showed relatively high abundance index indices during specific months. Several species were detected only in particular months or exhibited marked seasonal fluctuations in acoustic abundance index. Overall, the heatmap demonstrates substantial temporal variation in species occurrence and relative acoustic abundance index within the monthly acoustic communities.

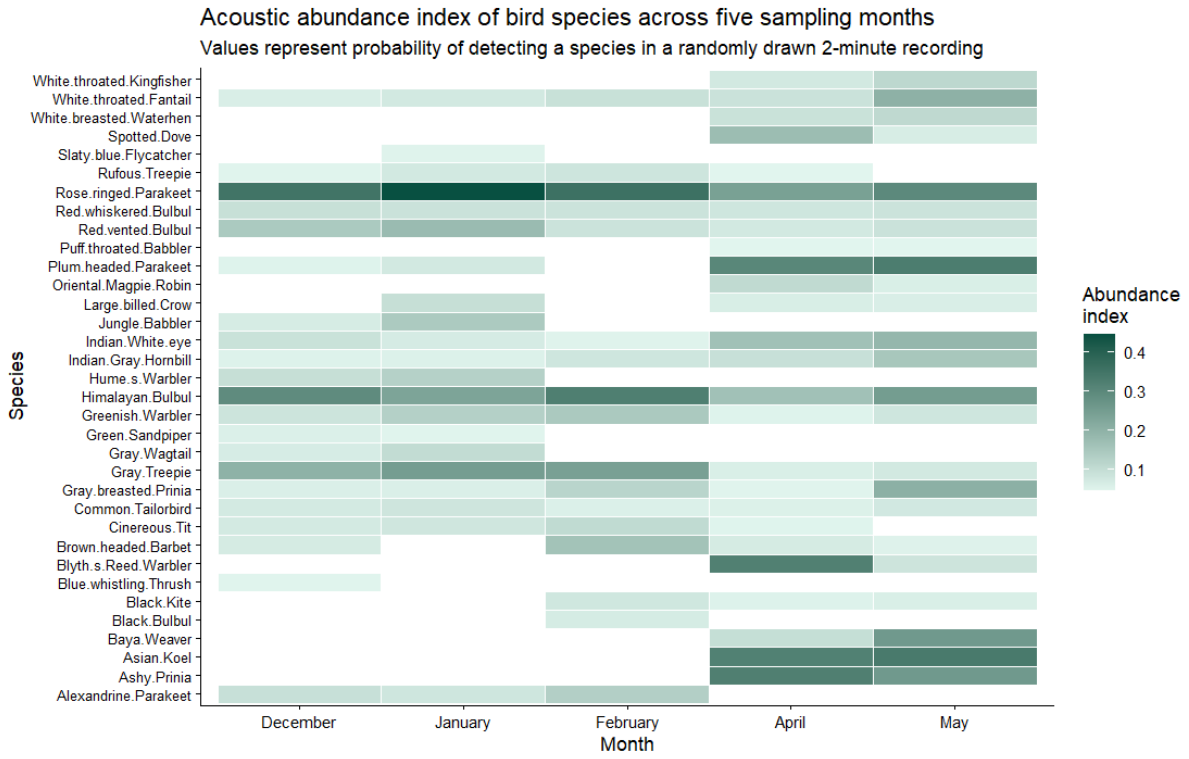


Figure 12.Heatmap of abundance index index of species across which has crossed 5% filter

Monthly differences in species composition of acoustic community

Acoustic community composition showed clear seasonal structure across the five sampling months. Pairwise Jaccard dissimilarity was highest between the summer months (April, May) and the winter months (December, January), with April vs December showing the greatest dissimilarity (0.667) and April vs May the least (0.087), indicating near-identical summer communities(Figure 13). Beta diversity decomposition revealed that dissimilarity was predominantly driven by species turnover rather than nestedness across most month pairs, with the exception of April-May where all dissimilarity was attributable to nestedness (turnover = 0.000), reflecting a stable resident breeding community across these months. Shannon diversity was highest in May (H' = 2.947) and lowest in February (H' = 2.645), with winter months showing intermediate values (December- 2.723, January-2.743), suggesting greater evenness of vocal activity during the breeding season (Figure 14).

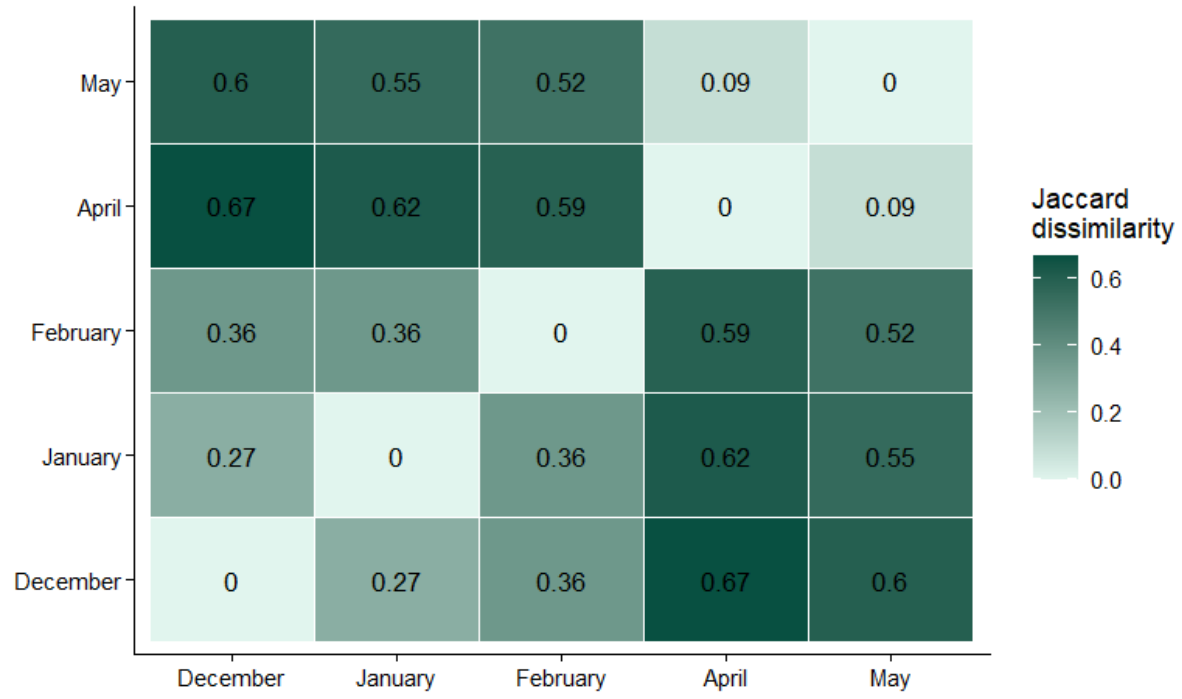


Figure 13- Pairwise Jaccard dissimilarity heatmap of acoustic community across sampling months

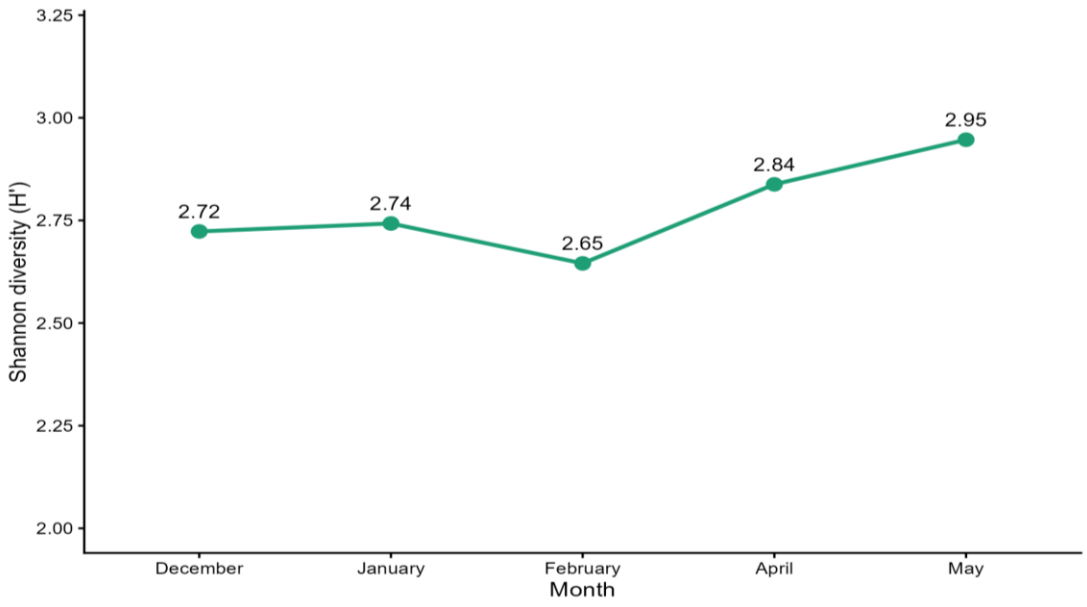


Figure 14- Shannon-Weiner Diversity Indices variation across five sampling months

Distribution of monthly acoustic communities in acoustic space

PCA of six acoustic parameters showed that species from all five months occupied largely overlapping regions of acoustic space (Figure 15). Monthly communities were broadly distributed along PC1, which primarily reflects frequency-related parameters, while PC2 captured temporal variation. . PCA of monthly species acoustic centroids showed that PC1 (53.1%) primarily represented frequency-related variation, whereas PC2 (19.4%) and PC3 (14.7%) represented temporal characteristics of vocalizations. MANOVA revealed no significant differences in acoustic niche space among months (Wilks' λ = 0.9765, F = 0.498, p = 0.916), and no pairwise month comparisons were significant after Bonferroni correction. Species distributions along the primary acoustic axis exhibited negative excess kurtosis and were frequently indistinguishable from uniform distributions in Kolmogorov-Smirnov tests (Table 7). Across all months, the distribution of species positions in acoustic space did not differ significantly from a uniform distribution (Shapiro–Wilk $p > 0.05$ in all months, except April which was marginal at $p = 0.071$), and the Kolmogorov–Smirnov test indicated 100% conformity with the expected uniform pattern. Negative excess kurtosis values in every month (-1.11 to -1.94) indicate relatively flat, evenly spread distributions rather than clustering, suggesting that species occupied acoustic space in a highly regular manner throughout the study period .As additional evidence of overdispersion in Winter and Summer community, the mean nearest-neighbor distance (NND) between winter and summer communities was 0.0344. This value was substantially lower than expected under the null model (mean ± SD = 1.2732 ± 0.2305). The observed NND was significantly lower than the null expectation ($Z = -5.375$, $p < 0.0001$), indicating that species in the winter and summer communities occupied more similar positions in acoustic space than expected by chance. Despite seasonal differences in species composition, the overall structure of the acoustic community remained largely conserved between seasons.

Table 7.Kolmogorov-Smirnov test results on Acoustic parameters

Month	N_species	SW_D	SW_p	Excess_kurtosis	KS_pct_uniform
December	8	0.879	0.1843	-1.704	100
January	10	0.868	0.0943	-1.539	100
February	10	0.939	0.5403	-1.114	100
April	8	0.837	0.0705	-1.937	100
May	10	0.93	0.4479	-1.242	100

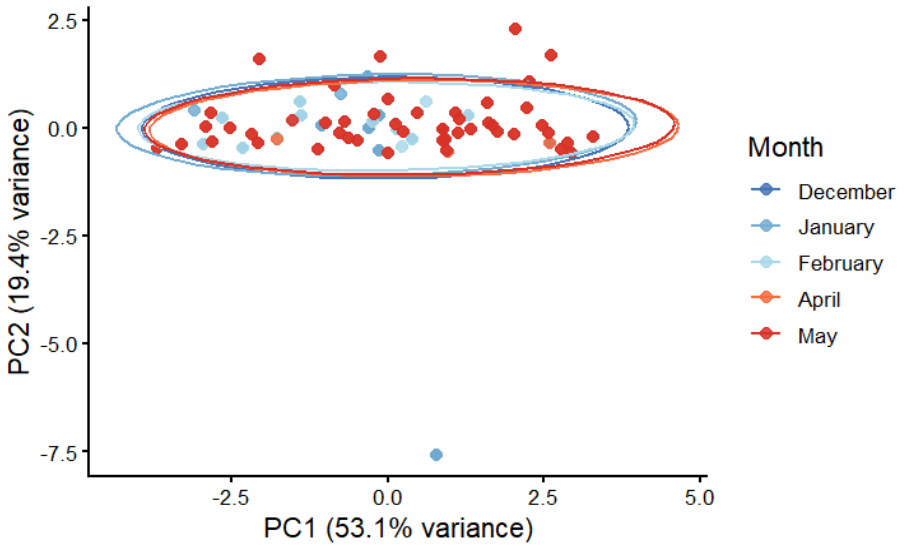


Figure 15.Species positions in acoustic parameter space across five sampling months in the Himalayan foothills

5. DISCUSSION

This study set out to understand how the seasonal arrival of Palearctic and Elevational winter migrants reshapes bird communities in the Himalayan foothills, examining three dimensions simultaneously; how richness and abundance index vary, how resident bulbuls forage, and is the acoustic community is organised. Across all three dimensions, the results point toward the same broad conclusion: the arrival of migrants changes which species are present and creates measurable seasonal rhythms in the community, but it does not appear to fundamentally disrupt the ecological arrangements that resident species have already established. The community absorbs the migratory influx and reorganises around it, rather than being destabilised by it in the study area.

The clearest evidence of seasonal change came from community composition and abundance index. Index of species richness and abundance index showed a descriptive peak in February, when migratory presence was at its highest, and declined through April as migrants departed. When site-level heterogeneity was explicitly accounted for using generalized linear mixed models with Site included as a random effect, index of species richness did not differ significantly across months ($\chi^2 = 4.50$, df = 4, p = 0.342). In contrast, abundance index varied significantly across months ($\chi^2 = 11.81$, df = 4, p = 0.019), with February showing the strongest increase relative to April. These results suggest that the arrival of migrants increased the number of individuals present in the community without producing a corresponding increase in the number of species. Such a pattern is ecologically plausible in migratory systems where incoming migrants augment an already species-rich resident assemblage. The random-effect variance associated with Site was low in both models, indicating that site-level differences contributed relatively little to the observed temporal patterns. These patterns suggest that while community composition was not strongly partitioned by month, a subtle directional change in assemblage structure occurred across the pre-migrant to post-migrant period, which was confirmed statistically by PERMANOVA .

Despite the non-significant richness result, community composition differed significantly across months confirming that seasonal reshuffling of species identity is real even when total index of species

richness remains relatively stable. The beta diversity results gave the most ecologically informative picture of how this reshuffling works. Turnover species replacing each other was the dominant component of dissimilarity across most month pairs, meaning that winter communities and summer communities are different primarily because different species are present, not because one is simply a depleted version of the other. This turnover-dominated pattern has been found consistently across bird systems in diverse habitats, including breeding birds on land-bridge islands in China (Si et al. 2015), birds along Himalayan elevational gradients (Ding et al. 2024), and waterbirds in Nigerian wetlands (Ekwemuka et al. 2025). It appears to be a general feature of bird communities that seasonal change is driven more by species replacement than by simple gain or loss. The one exception in this dataset was the April communities, which showed elevated nestedness in all pairwise comparisons meaning the April bird community was largely a subset of what was present in earlier months rather than a compositionally distinct assemblage. This pattern, where nestedness rises as migrants depart and the community contracts to its resident core, matches what Jin et al. (2026) found for montane birds in the Gyirong Valley of the Central Himalayas, where nestedness contributed nearly half of beta diversity in the non-breeding season as species were progressively lost from higher elevations. The April nestedness signal in this study is the clearest ecological fingerprint of migratory departure in the dataset.

Site identity remained a stronger predictor of community composition ($R^2 = 0.26$) than month ($R^2 = 0.09$), indicating that habitat heterogeneity within the campus exerts a substantial influence on community structure. Similar patterns have been reported from other heterogeneous landscapes. Gibru (2021) found no significant overall seasonal difference in avian composition or abundance index at Lake Hawassa wetlands in Ethiopia, while significant differences emerged between sites. In the Chitwan Annapurna Landscape in Nepal, physiographic zone explained more community differentiation than season (Bastola et al. 2025). On this campus, the mixture of sal forest, grassland, and managed green space creates fundamentally different bird communities at different sites, and this spatial heterogeneity remains an important driver of community organisation regardless of season. This can be considered an important conservation finding: maintaining habitat diversity within the campus appears to be more important for supporting overall avian diversity than any single seasonal factor.

Whether this seasonal community turnover translated into measurable competitive pressure on resident bulbuls was the central question of the second objective, and the answer is more complicated than the original hypothesis anticipated. The prediction was straightforward: more migrants should mean narrower niche breadth in resident bulbuls, as competition forces them to specialise. This is the pattern found by Jedlicka et al. (2006) in Mexico, Gbemiga (2014) in Ghana, and Chipley (1976) in Colombia, where resident birds narrowed their foraging height range or shifted to suboptimal foraging positions when migrants were present. The results here did not support this prediction. Instead, migratory index of species richness was positively associated with vertical and microhabitat niche breadth when more migrant species were present, bulbuls used a broader range of vertical strata and microhabitats, not a narrower range. Substrate and maneuver niche breadth showed no significant relationship with migratory abundance index in any direction, and insect biomass did not predict niche breadth in any dimension.

The most parsimonious interpretation of this result concerns the confounding role of mulberry fruiting. The period of lowest niche breadth in the data bi-weeks 7 to 10, corresponding to March and April coincided not with peak migration but with the fruiting of mulberry (*Morus sp*.) across the campus. All three bulbul species were observed aggregating at fruiting mulberry trees during this period. Because mulberry fruits at consistent low-to-mid canopy heights, the concentration of foraging activity at these trees would mechanically narrow vertical and microhabitat niche breadth regardless of what migrants were doing. This means the late-season niche contraction, the pattern that would most obviously support a story of competitive release as migrants depart cannot be attributed to competitive release with any confidence, because resource tracking around mulberry fruiting provides a direct, field-supported explanation. Fitzgerald et al. (2021) showed in subtropical Australian floodplain forests that avian community composition and guild representation responded strongly to seasonal fruit and nectar availability, with frugivore and nectivore guilds tracking phenological resource pulses closely. A similar resource-tracking dynamic appears to be operating here. Fruit availability in this study was recorded only as monthly presence or absence and could not be included as a statistical covariate, so this remains an interpretive inference rather than a statistically tested conclusion, but it is an inference strongly

supported by repeated field observations across multiple sites and all three bulbul species. The proposed role of mulberry fruiting in driving late-season niche contraction needs quantitative validation in future work that measures fruit abundance index continuously throughout the season.

An alternative explanation is that the positive relationship between migrant richness and niche breadth reflects spatial displacement rather than competitive specialisation. If migrants occupy certain preferred foraging positions for instance, warblers and flycatchers concentrated in the mid-canopy resident bulbuls may shift to both higher and lower strata, mechanically increasing measured niche breadth even though individual birds are not choosing to be generalists. Navarro-Velez and Dhondt (2025) note in a review of migrant-resident interactions in tropical birds that residents often show shifts in foraging height and microhabitat when migrants arrive, suggesting microhabitat displacement, and that this can increase intraspecific competition among residents as they crowd into similar positions. However, this explanation should be treated cautiously because the present study did not directly measure migrant occupancy of foraging strata, competitive interactions, or displacement behaviour. As such, it remains a plausible hypothesis rather than a demonstrated mechanism and requires targeted testing in future studies.

One pattern that does not fit neatly into either of these interpretations is the consistency of maneuver niche breadth throughout the study period. Unlike vertical and microhabitat breadth, maneuver breadth remained relatively stable regardless of whether migrants were present or absent, and regardless of whether mulberry was fruiting. This stability suggests that how bulbuls forage is more fixed than where they forage their repertoire of pecking, reaching, hanging, sallying and hovering occasionally is used at a similar breadth of frequencies across the whole season.

The stable isotope data from the non-breeding season (Figure 11) showed broadly overlapping isotopic niches among all three resident bulbul species, indicating similar dietary sources and trophic positions during this period. This high dietary overlap in isotopic space suggests that the three species are not strongly partitioning food resources at the trophic level during the non-breeding season. Field

observations of foraging prey type similarly showed no clear partitioning between species in the items consumed, with fruit dominating the diet of all three species throughout the study period.

Morphometric data collected from mist-netting sessions including tail length, secondary length, wing length, body weight, tarsus length, beak length, beak depth, and beak width are presented in Figure S1. The principal component analysis of these measurements shows that Red-vented Bulbul overlaps in morphological space with both Himalayan Bulbul and Red-whiskered Bulbul along PC1 (49.2% of variance) and PC2 (16.4% of variance). This morphological overlap suggests limited structural divergence in foraging apparatus among the three species, which would be expected to constrain resource partitioning through bill specialisation.

The phylogenetic context of these species adds an important interpretive layer. The three focal species are not a closely related species group that recently diverged in sympatry. Red-whiskered Bulbul (*P. jocosus*) belongs to a separate evolutionary lineage within *Pycnonotus*, while Red-vented Bulbul (*P. cafer*) and Himalayan Bulbul (*P. leucogenys*) share a more recent common ancestor. Their co-occurrence in the Himalayan foothills therefore represents secondary contact between lineages that diverged elsewhere. What the phylogeny does support is that these species have not been evolving together in the same habitat for their entire history, which is consistent with the observed lack of strong niche partitioning: they may not have had sufficient evolutionary time or competitive pressure in sympatry to diverge strongly in resource use.

Taken together, the isotopic, morphological, behavioural, and phylogenetic evidence points toward a low level of measurable interspecific competition among the three bulbul species at this study site. Two explanations deserve consideration. First, these species may be coexisting with limited competition because their evolutionary histories have already separated their core distributions at the biogeographic scale, and the Himalayan foothills represents a zone of secondary overlap where competitive exclusion has not yet or may never drive further niche divergence. Second, and more immediately, the peri-urban character of the WII campus may be masking competitive dynamics that would be visible in a natural forest context. Anthropogenic food subsidies - garden fruit, waste, and cultivated plants, may be

simultaneously reducing resource scarcity for all three species, relaxing competition to a level that would not exist in a closed-canopy forest with limited and seasonally variable food. Whether niche partitioning among these three species becomes detectable in a less disturbed forest landscape is an important and testable question for future work, and one that has direct relevance to understanding how urbanisation alters competitive dynamics within resident bird communities.

The acoustic results tell a story that is consistent with the foraging ecology results in one important respect: the resident community appears well-buffered against disruption by migratory influx. The MANOVA result ($p = 0.916$) found no significant difference in acoustic niche structure across months, meaning the distribution of species in acoustic parameter space did not change measurably between migrant-present and migrant-absent periods. The KS tests showed that species were overdispersed in acoustic space spread out more evenly than expected by chance and this overdispersion was consistent across all months. This is a positive finding that supports the Acoustic Niche Hypothesis (Krause 1993), the idea that species partition acoustic space to reduce communicative interference. Krishnan (2019), studying an urban dry deciduous scrub-grassland in peninsular India, found the same pattern overdispersed acoustic communities that maintained their structure across seasons including when winter migrants were present and concluded that migrants fit into the same acoustic niche space already used by residents rather than disrupting it. Lahiri et al. (2021) found convergent overdispersed distributions across two very different South Asian grassland biomes, suggesting that acoustic niche partitioning is a robust community-level property in Indian bird assemblages. The present study adds a Himalayan foothill context to this small but growing body of evidence.

The NND result ($Z = -5.375$, $p < 0.0001$) adds an additional layer to this picture. Even though the Jaccard dissimilarity results showed that winter and summer species compositions are quite different the two seasons have largely different species lists the winter and summer acoustic communities occupied more similar positions in acoustic parameter space than a null model would predict. This means that as species turn over between seasons, new species slot into acoustic positions similar to those of the species that departed. The acoustic structure of the community is conserved even though the species producing that structure change. Whether this reflects active acoustic adjustment by arriving

migrants, or simply reflects the physical properties of the habitat filtering which signal characteristics carry well, cannot be determined from this dataset. Both mechanisms are plausible and both would produce the same observed pattern.

Taken together, the methodological limitations of this study point in consistent directions for future work. The first limitation is very less spatial replication. The high within-month, between-site variance that reduced statistical power for richness index and abundance index tests could be addressed by either increasing the number of site visits per month. Also the point count has done without any fixed species richness and the time that point count data has taken was longer so that counts were not corrected for imperfect detection, that repeat counts of the same individual across the 15-minute window cannot be ruled out, and that consequently these are best interpreted as relative/comparative indices rather than absolute estimates. For the foraging niche analysis, the single most important improvement would be continuous, quantitative measurement of fruit availability at each site throughout the study period, so that fruit abundance index can be included as a statistical covariate alongside migrant abundance index and insect biomass. Without this, the confounding of competitive release with resource tracking around mulberry fruiting cannot be statistically resolved. Extending the study period to include October-November (pre-arrival) and June (post-breeding) would also substantially increase the number of biweekly data points and improve the power of the niche breadth models. For the acoustic analysis, two limitations need honest acknowledgement. Using species mean acoustic parameters pooled across the entire study period assumes that each species vocalises identically in all months, which may not be true extracting parameters separately for each month would allow within-species acoustic flexibility to be detected. And supplementing AudioMoth recordings with Xeno-Canto calls for species where field recording quality was insufficient introduces a source of measurement error that is difficult to quantify.

Despite these limitations, this study provides something that did not previously exist for this region: a quantitative, multi-dimensional baseline of how the avian community at a Himalayan foothill site changes across the full arc of Palearctic migratory influx and departure. The results suggest that in a structurally diverse, habitat-heterogeneous site like the WII campus, the resident community has sufficient ecological flexibility to absorb the migratory influx without measurable competitive

disruption not because competition is absent, but because the community appears buffered by habitat diversity, dietary generalism in the focal resident species, and the conserved structure of the acoustic niche space. The dominant message from all three objectives is one of community resilience rather than community disruption. As Palearctic migratory populations face accelerating declines and climate change alters the timing of both migration and resource phenology, this baseline will become increasingly valuable for detecting and interpreting ecological change in one of the world's most important, and most understudied, avian wintering regions.

6. CONCLUSION

This study contains temporally resolved investigation of resident avian community responses to Palearctic and elevational migratory influx in the Himalayan foothills of Dehradun. Across three ecological dimensions - community structure, foraging ecology, and acoustic organisation -the results point toward a common theme: the resident community at the Wildlife Institute of India campus may have absorbing the annual migratory influx without measurable structural disruption, suggesting ecological resilience rather than competitive destabilisation.

Avian community composition shifted significantly across months, driven predominantly by species turnover rather than nestedness, with the April community revealing the clearest fingerprint of migratory departure as it contracted to a resident core. Contrary to prediction, resident bulbuls did not narrow their foraging niche breadth during peak migratory abundance index; instead, vertical and microhabitat breadth were positively associated with migrant presence, a pattern best explained by confounding by mulberry fruiting phenology rather than competitive specialisation. The acoustic community maintained overdispersed structure consistently across months, and winter and summer species compositions occupied more similar acoustic space than expected by chance, suggesting that acoustic niche structure is conserved even as species composition turns over seasonally.

These findings establish a quantitative ecological baseline for this understudied flyway. As Palearctic migratory populations face accelerating declines and climate change reshapes the phenology of both migration and resource availability, this baseline will be essential for detecting and interpreting future ecological change in one of the world's most important avian wintering regions

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SUPPLEMENTARY MATERIAL

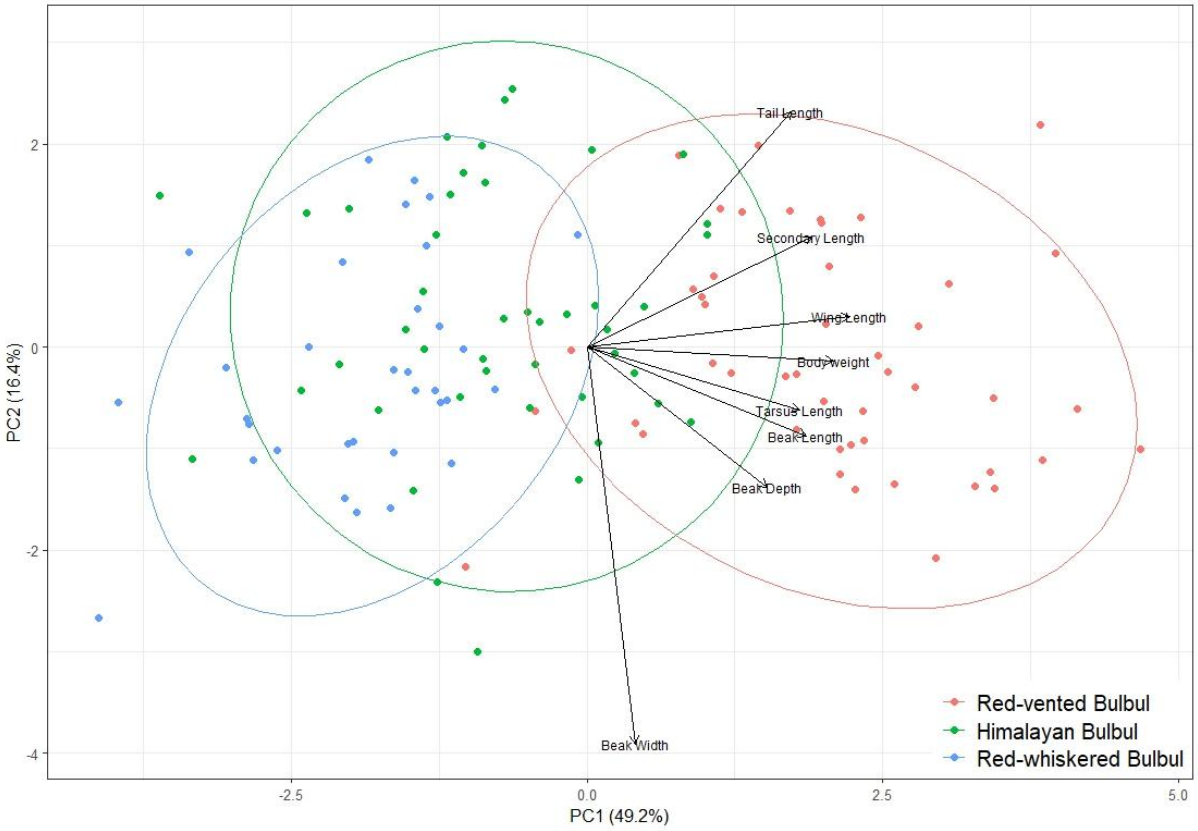

Figure S1. PCA visualization of PC1 and PC2 of morphometrical parameters of three resident bulbuls from WII Campus.