

RESEARCH ARTICLE

Increasing species richness along elevational gradients is associated with niche packing in bat assemblages

Rohit Chakravarty^{1,2}  | Viktoriia Radchuk¹  | Shreyas Managave³  |
Christian C. Voigt^{1,2} 

¹Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

²Department of Animal Behaviour, Institute of Biology, Freie Universität Berlin, Berlin, Germany

³Department of Earth and Climate Science, Indian Institute of Science Education and Research (IISER) Pune, Pune, India

Correspondence

Rohit Chakravarty

Email: rohit.chakravarty77@gmail.com

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Abstract

1. The change in species richness along elevational gradients is a well-known pattern in nature. Niche theory predicts that increasing species richness in assemblages can either lead to denser packing of niche space ('niche packing') or an expansion into its novel regions ('niche expansion'). Traditionally, these scenarios have been studied using functional traits but stable isotopes provide advantages such as identifying the degree of resource specialisation, or niche partitioning among functionally similar species.
2. In this study, we evaluate the relevance of niche packing versus niche expansion by investigating stable carbon and nitrogen isotopic niche width and overlap among 23 bat species from six functional groups across a 1500 m elevational gradient in the Himalaya.
3. Our results suggest that an increase in species richness in the low elevation is accompanied by small niche width with high overlap, whereas the high elevation assemblage shows large niche width with low overlap among functional group members. At the functional group level, edge-space foraging, trawling, and active gleaning bats have the highest niche width while passive gleaning bats that are only found in high elevations are isotopic specialists showing low overlap with other groups. Edge and open-space foraging bats showed idiosyncratic changes in niche width across elevations. We also find that the niches of rhinolophid bats overlap with edge-space and open-space foraging bats despite their unique functional traits.
4. These results support the idea that at low elevations high species richness is associated with niche packing while at high elevations strong niche partitioning prevails in dynamic and resource-poor environments. We conclude that although high elevation animal assemblages are often 'functionally underdispersed', that is show homogenous functional traits, our approach based on stable isotopes demonstrates niche partitioning among such functionally similar species.

KEYWORDS

bats, elevational gradients, Himalaya, niche expansion, niche packing, stable isotopes

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1 | INTRODUCTION

Latitudinal and elevational gradients in diversity are widespread patterns across taxa and geographical regions. Typically, species richness is highest at low latitudes and elevations (McCain & Grytnes, 2010). MacArthur (1965) argued that two contrasting patterns of niche occupancy may help explain these changes in species richness (Pellissier et al., 2018; Pigot et al., 2016), wherein 'niche' is defined as an n -dimensional hypervolume comprising all abiotic and biotic elements that allow a species to exist (Hutchinson, 1957). Under MacArthur's first model called 'niche expansion', an increase in species richness is associated with species occupying novel regions of the niche space of the assemblage. In contrast, the 'niche packing' model suggests that an increase in species richness leads to denser packing of the assemblage niche space due to finer specialisation or increased overlap (MacArthur, 1965; Paganí-Núñez et al., 2019; Pellissier et al., 2018; Pigot et al., 2016). There is poor understanding of which of these two mechanisms structures assemblages of various taxa across latitudinal and elevational gradients.

A global model for birds predicts that niche packing with high niche overlap occurs in areas of high net primary productivity (Pellissier et al., 2018). This observation is supported in local-scale studies along elevational gradients where niche packing is seen at low elevations (Pigot et al., 2016; Schumm et al., 2020). Old (basal) or early colonising lineages diversify and expand the community niche space while new (derived) lineages get packed within the 'boundaries' created by old lineages (Hughes et al., 2021; Tanentzap et al., 2015). The most common method of investigating niche occupancy is to measure how the diversity of functional traits in communities changes with species richness across the gradient of interest (Pellissier et al., 2018; Pigot et al., 2016). Functional traits such as morphological, physiological, and life history traits of organisms are correlated with their functions in the ecosystem (Nock et al., 2016). With the easy availability of comprehensive trait datasets like Elton Traits (Wilman et al., 2014) and AVONET (Tobias et al., 2022), the applications of trait-based ecology will undoubtedly grow. However, functional traits do not always accurately delineate feeding guilds at finer spatial scales, nor do they reliably predict specialisation on food resources (Pigot et al., 2016; Weiss & Ray, 2019). These shortcomings can be overcome by using dietary tracers like stable isotopes.

Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in animal tissues are reliable proxies for an animal's niche breadth (Bearhop et al., 2004; Ben-David & Flaherty, 2012). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values vary predictably across photosynthetic pathways, habitats, and trophic levels. 'Isotopic niche' is then defined as the space that an animal occupies within the space determined by these isotopic values (Martínez Del Rio et al., 2009; Newsome et al., 2007). The isotopic niche differs from dietary niche because it is measured by the diversity of isotopically unique resources rather than taxonomically unique prey species. For example, an isotopic specialist may not necessarily be a dietary specialist because it may feed on the same mixture of isotopically distinct resources (as opposed to the same set of prey species). Also, if an animal specialises on prey items with

widely divergent isotopic compositions, it will show up as an isotopic generalist (Martínez Del Rio et al., 2009; Newsome et al., 2007).

Stable isotope analysis is of great potential for assessing the niche breadth and overlap of elusive animals like bats. $\delta^{13}\text{C}$ values vary between C_3 versus C_4 , aquatic versus terrestrial plants and so on (Schulting, 1998). Therefore, they indicate the basal nutrition sources of the food chain. $\delta^{15}\text{N}$ values increase with trophic level. Together, these two isotopes tell us which food chains different bats feed on and how they partition resources across food chains and trophic levels. Bat assemblages are extremely diverse (Kingston et al., 2003; Rex et al., 2008), and it is impossible to ascertain the variety of insect prey species that they consume from direct observations or conventional pellet analysis. For example, species that were conventionally thought to be solely frugivorous or insectivorous seem to be omnivorous based on isotopic data (Oelbaum et al., 2019; Rex et al., 2015). Further, stable isotope analysis includes regions of the trophic niche not covered by conventional diet analysis. For example, forest bats that forage at different vegetation strata, such as ground or canopy level, can be distinctly separated using stable isotope analysis but not based on conventional diet analysis (Voigt et al., 2015). Previous studies comparing regions of high and low bat diversity show that there is high intra- and inter-guild overlap in isotopic niches in areas of high diversity (Monadjem et al., 2018; Oelbaum et al., 2019). Bats belonging to the open-space foraging guild typically show large niches with high intra-guild overlap (Ruadreo et al., 2019; Voigt et al., 2015). However, studies also point to niche partitioning in interesting ways. For example, Neotropical fruit-eating bats show vertical stratification in foraging habitats (Rex et al., 2011) and two European congeneric species in their sympatric range feed on insects belonging to different trophic levels (Siemers et al., 2011). Only one study has compared niche partitioning between two sites of high and low diversity in Africa and observed niche packing in the high diversity site with presumably higher productivity (Monadjem et al., 2018). We do not know if these patterns hold across geographical regions, species pools, elevational or anthropogenic gradients.

In this study, we used stable carbon and nitrogen isotopes to measure the isotopic niches of bat functional groups and communities across a 1500m elevational gradient in Kedarnath Wildlife Sanctuary (Kedarnath WLS) in western Himalaya. Previous research along this gradient has shown that species richness declines at the highest elevation, but functional dispersion is lower than expected both at the highest and the lowest elevations indicating dense packing of the functional trait space (Chakravarty et al., 2021). The bats in Kedarnath WLS can be classified into seven functional groups (Denzinger et al., 2016), as follows: (a) Edge-space aerial foragers ('edge-space foraging bats'), (b) Edge-space trawling foragers ('trawling bats'), (c) Fruit-eaters, (d) Narrow-space active gleaning foragers ('active gleaning bats'), (e) Narrow-space flutter detecting foragers ('flutter-detecting bats'), (f) Narrow-space passive gleaning foragers ('passive gleaning bats') and (g) Open space aerial foragers ('open-space foraging bats') (described in Table 1). With respect to isotopic niches of the functional groups, we predicted that (a) edge and

TABLE 1 Detailed classification of our study species into functional groups following Denzinger et al. (2016). Samples sizes of each species and their functional groups are mentioned for low, intermediate, and high elevations. Functional groups with $n < 3$ (highlighted with asterisks) were removed from the calculations of SEAb and niche overlap.

Functional group	Species	Low elevation	Intermediate elevation	High elevation
Edge-space aerial foragers (Edge-space foraging bats)	(i) <i>Arielulus circumdatus</i>	1	0	1
	(i) <i>Barbastella darjelingensis</i>	2	0	1
	(i) <i>Hypsugo affinis</i>	1	0	0
	(i) <i>Miniopterus fuliginosus</i>	2	0	0
	(i) <i>Mirotrellus joffrei</i>	19	1	0
	(i) <i>Myotis muricola</i>	3	3	3
	(i) <i>Myotis sicarius</i>	1	0	0
	(i) <i>Myotis siligorensis</i>	1	0	0
	(i) <i>Pipistrellus cf. ceylonicus</i>	37	3	1
	(i) <i>Submyotodon caliginosus</i>	0	0	1
		$n = 67$	$n = 7$	$n = 7$
Edge-space trawling foragers (Trawling bats)	(i) <i>Myotis longipes</i>	12	0	0
Fruit-eaters	(i) <i>Sphaerias blanfordi</i>	0	1	1
		$n = 0$	$n = 1^*$	$n = 1^*$
Narrow-space active gleaning foragers (Active-gleaning bats)	(i) <i>Murina aurata</i>	2	1	2
	(i) <i>Murina huttoni</i>	0	1	0
		$n = 2^*$	$n = 2^*$	$n = 2^*$
Narrow-space flutter detecting foragers (Flutter-detecting bats)	(i) <i>Rhinolophus lepidus</i>	5	1	0
	(i) <i>Rhinolophus luctus</i>	2	0	0
	(i) <i>Rhinolophus pearsonii</i>	1	4	0
	(i) <i>Rhinolophus sinicus</i>	2	3	0
		$n = 10$	$n = 8$	$n = 0$
Narrow-space passive gleaning foragers (Passive-gleaning bats)	(i) <i>Plecotus homochrous</i>	0	2	11
	(i) <i>Plecotus wardi</i>	0	0	9
		$n = 0$	$n = 2^*$	$n = 20$
Open-space aerial foragers (Open-space foraging bats)	(i) <i>Eptesicus pachyomus</i> (formerly <i>E. serotinus</i>)	3	0	0
	(i) <i>Nyctalus leisleri</i>	12	9	2
	(i) <i>Nyctalus cf. noctula</i>	0	1	0
	(i) <i>Tadarida cf. teniotis</i>	1	0	0
		$n = 16$	$n = 10$	$n = 2^*$

open-space foraging bats would occupy the central portion of the assemblage niche space, and have the broadest, yet most overlapping isotopic niches (cf. Ruadreo et al., 2019; Voigt et al., 2015); (b) trawling, passive and active gleaning bats would occupy different peripheral portions of the assemblage niche space and have narrow niche widths in concordance with their unique feeding behaviours; (c) the extreme trait differences of flutter-detecting bats would not result in a unique isotopic niche (cf. Voigt et al., 2015). Based on previous studies (cf. Monadjem et al., 2018; Pellissier et al., 2018; Pigot et al., 2016), we predicted that (d.i) we would observe niche packing at the low elevation, species-rich site due to its presumably high productivity. However, the lowest elevation had the highest number of species of edge-space foraging bats, and trawling bats were also exclusively found there. Both of these functional groups

are predicted to have large niche width, and therefore (d.ii) isotopic niche expansion could also be seen at low elevations whereas, (e) low species richness at the highest elevation would be accompanied by small niche width with or without high overlap (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in Kedarnath Wildlife Sanctuary (30°25'–30°41'N, 78°55'–79°22'E) situated in the state of Uttarakhand in the western Himalaya of India (see map of study site at: <https://www.nature.com/articles/s41598-021-01939-3/figures/1>).

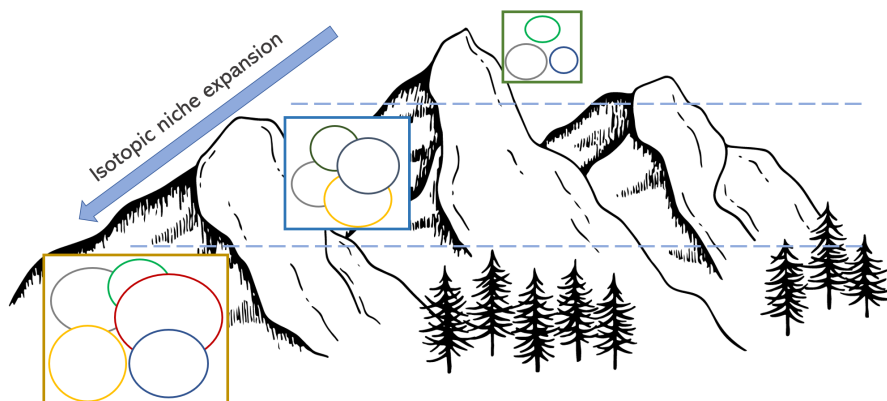


FIGURE 1 Schematic representation of our hypotheses. Each box represents an assemblage of bats and the ellipses represent the isotopic niches of its constituent bat functional groups. We predict that an expansion of isotopic niches is witnessed as species and functional group richness increase towards the lowest elevation. Vector art freely downloaded from <https://www.canva.com/>.

The sanctuary covers an elevational gradient from 1400m to 4000m above sea level (a.s.l.) with changes in the dominant vegetation. At low elevations, the forest is classified as 'Himalayan moist temperate' and is dominated by *Quercus* spp., while sub-alpine forests above 2800m are dominated by *Rhododendron* spp. The tree-line ends above 3000m leading into alpine meadows (Champion & Seth, 1968). The sanctuary harbours 28 species of bats (Chakravarty et al., 2020, 2021).

2.2 | Field work

We sampled at the following four locations across the elevational gradient: Mandal (1500–1800m), Ansuya (2000–2200m), Chopta (2700–3000m) and Tungnath (3300–3700m) but we had to exclude Tungnath from the analysis due to low sample sizes. The former three elevations are subsequently referred to as 'low' (Mandal), 'intermediate' (Ansuya) and 'high' (Chopta). Sampling was conducted between late March and mid-May in 2018, 2019 and 2021 coinciding with summer in the Himalaya, and preceding the onset of the monsoon season (https://mausam.imd.gov.in/imd_latest/contents/monsoon.php). We caught bats using thin nylon and monofilament mistnets of 4, 6, and 9 m length, 16 × 16 and 19 × 19 mesh sizes (Ecotone GOC) for 4h following dusk (starting between 18:30h in early summer and 19:30h in late summer). The captured bats were identified to species level following published studies and keys (Bates & Harrison, 1997; Chakravarty et al., 2020; Srinivasulu et al., 2010). From each bat, we collected two wing biopsies (one from each wing at roughly the same position) using a sterilised biopsy punch of 4 mm diameter. We dry stored the wing biopsies in vials containing silica gel crystals. The wing tissue samples were used for stable carbon and nitrogen isotope analysis to investigate isotopic niches of our study species. After collecting these samples, we released the bats at their site of capture.

In order to characterise the basal stable carbon and nitrogen isotope ratios at different elevations we collected plant and insect samples for stable isotope analysis. We collected one leaf each from 20 individual *Quercus* spp. and 20 individual *Rhododendron* spp. (the dominant tree species across the elevational gradient) at each elevation (low, intermediate, and high). Using a custom-made ultraviolet

light-based trap, we collected 21, 21, and 17 nocturnal insects (predominantly Lepidoptera) at low, intermediate, and high elevation respectively.

We handled all live bats following the guidelines of the American Society of Mammalogists (Sikes, 2016). Fieldwork was further approved by the Internal Committee for Ethics and Animal Welfare, Institute for Zoo and Wildlife Research (approval no. 2018-06-01), and conducted under a permit issued by the Uttarakhand State Forest Department, Government of India (permit no. 2261/5-6). Wing tissue samples were exported from India to Germany following the approval of the National Biodiversity Authority, Government of India in accordance with the Nagoya Protocol (permit no. Form B/79/18/18-19/5041).

2.3 | Laboratory analysis

We analysed the wing tissue samples at the stable isotope facility of the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. We put the wing tissue samples into 1:2 methanol-trichloromethane solution for 24 h to clean surface contaminants. After 24h, the solution was drained off and the tissue samples were dried in an oven at 50°C for more than 48 h. We then loaded the samples into tin capsules (IVA Analysentechnik) and folded them tightly. Due to the size and wing density differences of the different bat species, our sample weights ranged from 100 to 580mg. The samples were measured using an isotope ratio mass spectrometer (IRMS, Delta V Advantage; Thermo Fisher) in continuous flow coupled to an elemental analyser (Flash EA 1112 Series; Thermo Fisher) via a ConFlo III device (Thermo Fisher). Isotope ratios were expressed using the delta notation ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) as parts per mille deviations from the international standards Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen (Air N_2) respectively (given by the equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$). Samples were measured together with in-house protein standards of tyrosine ($\delta^{13}\text{C} = -24.0\text{‰}$, $\delta^{15}\text{N} = 4.4\text{‰}$) and leucine ($\delta^{13}\text{C} = -30.3\text{‰}$, $\delta^{15}\text{N} = 11.0\text{‰}$) for drift and calibration purposes.

We punched the leaf samples using a sterilised hole punch. The punches were collected in vials and powdered using a tissue homogeniser (Next Advance). We packed ~1 mg of powdered plants for carbon and nitrogen analysis. Insect samples were subjected to the

same washing and drying procedure as wing tissue samples, following which they were packed into tin capsules. IRMS facility at the Indian Institute of Science Education and Research Pune was used for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements of the leaf and insect samples. The IRMS (Isoprime 100; Isoprime, Elementar) attached to Vario Pyro cube elemental analyser (Elementar) was used for this. The repeatability and accuracy were assessed by analysing laboratory standards: sucrose I ($\delta^{13}\text{C} = -12.1\text{‰}$), sucrose II ($\delta^{13}\text{C} = -26.7\text{‰}$), sulfanilamide ($\delta^{13}\text{C} = -27.8\text{‰}$, $\delta^{15}\text{N} = -6.3\text{‰}$) and ammonium sulfate (USGS 25) ($\delta^{15}\text{N} = -30.41\text{‰}$). Insect samples were subjected to the same washing and drying procedure as wing tissue samples, following which they were measured in the same process as described above. The accuracy of the measurements was the same as described for the other laboratory.

2.4 | Statistical analysis

We tested differences in baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (plant and insect samples) in assemblages across elevations by performing a permutational ($n = 999$) multivariate analysis of variance (perMANOVA) using the 'adonis' function of 'VEGAN' R package (Oksanen et al., 2019). The perMANOVA was performed using Gower distances between isotopic values (continuous variable) and elevational assemblage (categorical variable).

We pooled bat species into the seven functional groups as described in Section 1 (Denzinger et al., 2016). The group membership of our study species and their sample sizes are detailed in Table 1. Fruit-eating bats had to be removed from all analyses as we only caught one individual each at intermediate and high elevations. Active gleaning bats could only be used for calculating functional group niche width across elevations.

We estimated functional group niche width, by computing Bayesian standard ellipse areas (SEAb) in two ways: (i) for each functional group within each elevation and (ii) across elevations, by pooling the data per functional group together (so as to increase the sample size). SEAb were estimated with the R package SIBER ver. 2.1.6 (Jackson et al., 2011). We tested whether elevation affects each functional group niche width differently, by fitting a linear model (normal distribution and identity link) with the functional group niche width as response and elevation, functional group identity and an interaction among them as predictors. We tested the robustness of our findings with respect to the sample size by subsampling the data to four samples per functional group at each elevation.

We calculated assemblage niche width as distance to centroid of the convex polygon using Bayesian Layman metrics (Layman et al., 2012) implemented in the SIBER package. Additionally, we measured nearest-neighbour distance as an estimate of 'packing' within the niche space. We calculated these metrics with 50 iterations and assessed the difference across elevational communities using a general linear model (GLM) and post-hoc Tukey's Honest Significance Difference (HSD) test. We chose to use 50 iterations because a

higher number would have strongly inflated the sample sizes, invariably causing the differences to be significant. The bare minimum to run these analyses are three samples per functional group at any given location. Therefore, we had to exclude active gleaning bats and fruit bats from this analysis.

We assessed the statistical significance of niche overlap with elevation using a linear mixed effects model (normal distribution and identity link), with response being niche overlap per functional group, and predictors being elevation, functional group identity, and their interaction. We included a combination of functional groups for which the overlap was calculated as random intercept in the model, so as to account for variation in niche overlap among different functional groups. The model was fitted to the data generated with 40 permutations of niche overlap probabilities (calculated using the R package NICHEROVER ver. 1.10; Swanson et al., 2015) between all functional group combinations at each elevation. We chose 40 iterations so as to not inflate the significance merely due to a higher sample size. We then used likelihood ratio test (LRT) to test for the effect of elevation on niche overlap. While calculating niche overlap of functional groups at each elevation, we had to exclude active gleaning bats from the low elevation assemblage, fruit bats, active and passive gleaning bats from intermediate elevation assemblage, and fruit bats, active gleaning, and open-space foraging bats from high elevation assemblage due to low sample sizes. Since population densities of bats from these functional groups were low, we did not expect their presence or absence to strongly affect the niche packing of communities.

3 | RESULTS

When comparing the baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from plant samples collected across the elevational gradient, we observed significant differences in the dispersion of plant isotopic values between low and high elevations (Tukey's HSD $p < 0.01$) (Figure S1, Table S1). Such differences were not seen in the samples of Lepidopteran insects collected at the three elevational communities (Tukey's HSD, $p = 0.94$) (Figure S2).

Isotopic biplots of raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figure 2) provide a visual estimate of niche width and niche overlap in bat communities at different elevations. The bat assemblage at high elevation had significantly higher isotopic niche width (measured as distance to centroid) and nearest-neighbour distance than at intermediate and high elevations (Figure 3; Tukey's HSD $p < 0.01$). The niche width and nearest-neighbour distance of bat assemblages at low and intermediate elevations did not differ significantly (Figure 3; Tukey's HSD $p = 0.88$). At the functional group level, edge-space foraging, trawling and active gleaning bats had the highest SEAb (calculated across elevations) and the differences among them were not significant (Figure 4; Tukey's HSD $p > 0.5$). SEAb in the other three functional groups significantly decreased in the following order: open-space foraging > flutter-detecting > passive gleaning bats (Figure 4; Tukey's HSD $p < 0.05$). We found a significant interaction between elevation and functional group

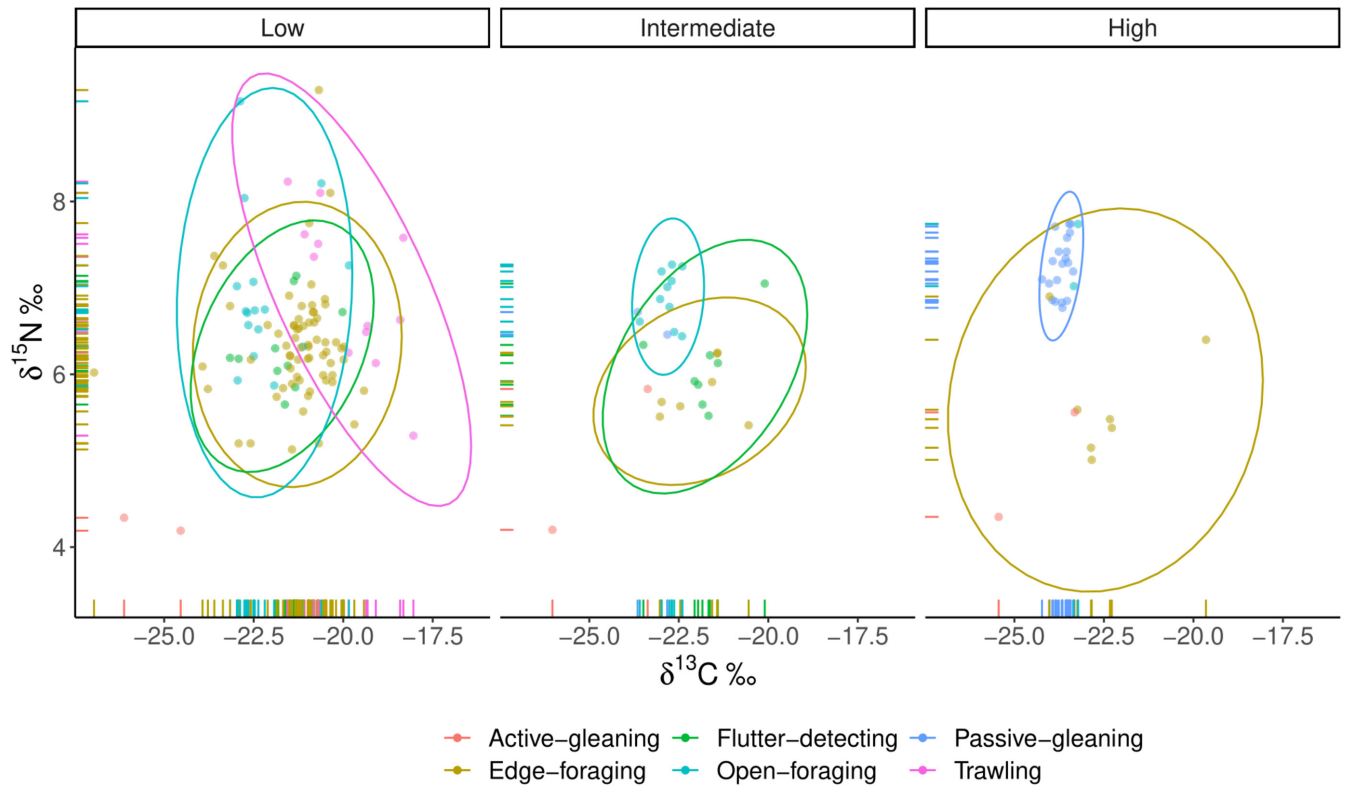


FIGURE 2 Isotopic biplots of raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) plotted for bat assemblages across elevations. Ticks along the margins show the density of data points per functional group. Standard ellipse areas are plotted for different functional groups as indicated in the legend.

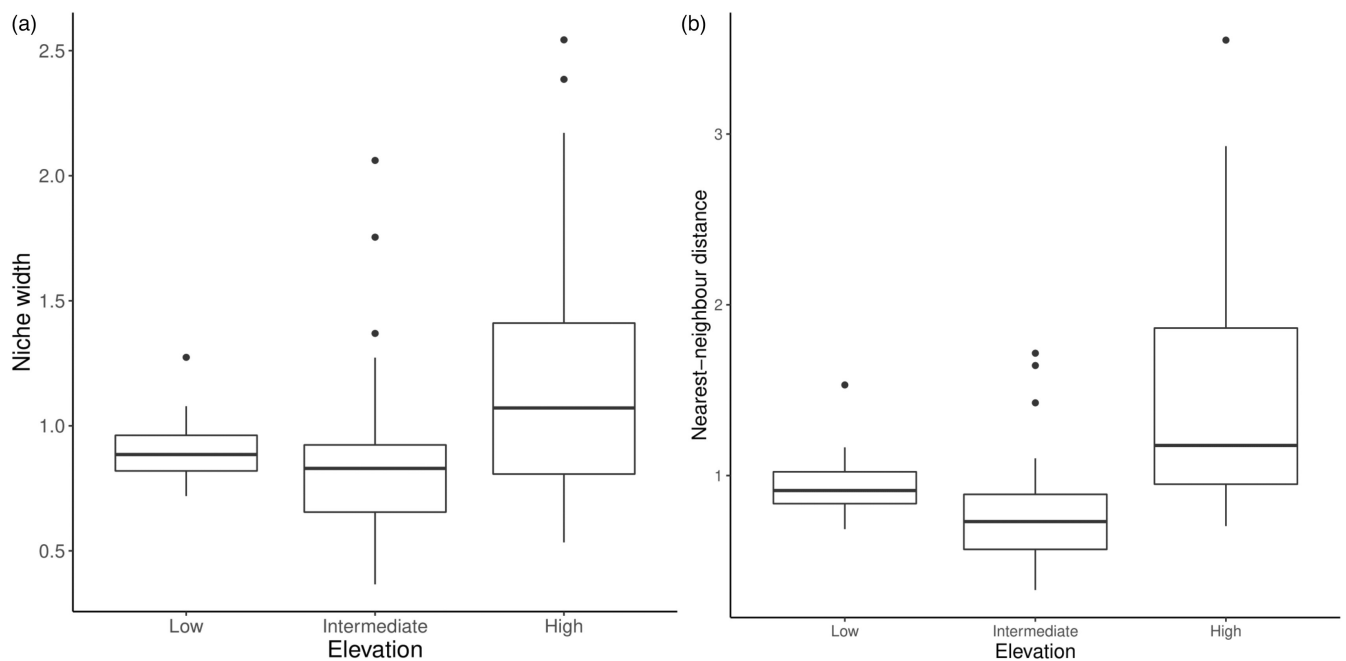


FIGURE 3 Variation in (a) isotopic niche width (measured as distance to centroid of the assemblage niche space), and (b) Nearest-neighbour distance among functional groups in bat assemblages across elevations. The bold horizontal line represents the median, the box depicts the inter-quartile range, and the whiskers show the lower and upper quartiles. Points beyond the whiskers are outliers.

niche width ($F = 8.4$, $df = 2$, $p < 0.001$; **Figure 5**), meaning that the niche width of specific functional groups changed across elevation. Our results were qualitatively similar with a reduced sample size of four individuals per functional group per elevation (**Figure S3**).

Isotopic niche overlap probability was high among bat species belonging to the functional groups of edge-space foraging, open-space foraging and flutter-detecting bats both across elevations and at each specific elevation (**Figure 2**; **Figure S4**). This overlap

FIGURE 4 Isotopic niche width (measured as Bayesian standardised ellipse areas) of functional groups calculated across elevations and plotted from left to right according to decreasing median values. The bold horizontal line represents the median, the box depicts the inter-quartile range, and the whiskers show the lower and upper quartiles. Points beyond the whiskers are outliers. The inset shows the raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) and their distributions along the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ axes. Colours in the inset correspond to colours of functional groups in the boxplot.

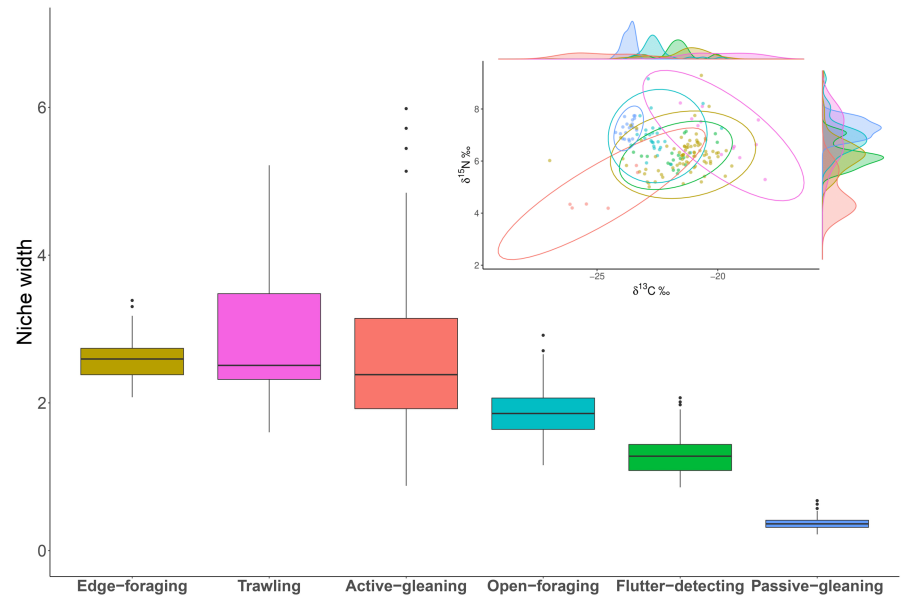
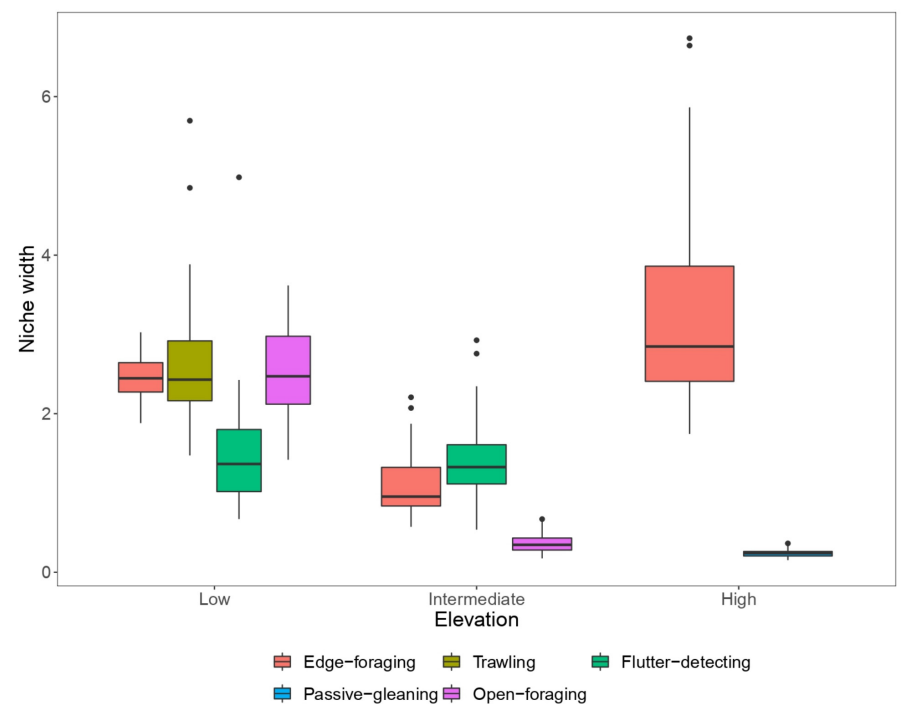


FIGURE 5 Change in niche width (measured as SEAb) of functional groups with elevation.



was predominantly along the $\delta^{15}\text{N}$ scale and not along the $\delta^{13}\text{C}$ scale (Figure 4). Trawling, passive gleaning and active gleaning bats occupied peripheral portions of the isotopic niche space of assemblages and showed low overlap with other functional groups (Figures 2 and 4; Figure S4). At low elevation, the mean overlap probability between all functional groups (except for trawling bats) was above 50% (Figure 2; Table S2). At intermediate elevation, we observed an average niche overlap probability of 68% between edge-space foraging and flutter-detecting bats, but only 30% and 8.5% between open-space foraging bats with flutter-detecting and edge-space foraging bats respectively (Figure 2; Table S3). At high elevation, we estimated an average overlap probability of 28% between passive gleaning bats and edge-space foraging bats,

the two functional groups for which we had sufficient samples (Figure 2; Table S4). Our mixed effects model showed that niche overlap was significantly higher at the low elevation (mean \pm SE estimate: $\beta = 0.39 \pm 0.19$) compared to the intermediate and high elevations ($X^2 = 323.22$, $df = 2$, $p < 0.01$; estimates \pm SE for intermediate and high elevations are, respectively: 0.01 ± 0.19 and 0.17 ± 0.17).

4 | DISCUSSION

We investigated isotopic niche width of bat assemblages and niche overlap of bat functional groups across a 1500m elevational

gradient with decreasing species richness at higher elevations. According to our predictions, we observed niche packing at the species-rich low elevation with high niche overlap among functional groups. In contrast, the species-poor highest elevation assemblage showed large niche width with low overlap among functional groups. At the functional group level, we predicted large niche width for edge- and open-space foragers, and peripheral niches for all other functional groups. We obtained mixed results.

4.1 | Niche packing versus expansion

With increasing species richness at low elevation, we observed a reduction in bat assemblage niche width and a significant increase in niche overlap indicating niche packing. Niche packing in our community occurs because within assemblages the 'boundaries' of the niche space are made up of functional groups that are common to all elevations. The species that are added in the low elevation assemblage get densely packed within this boundary. This packing can largely be attributed to the wide and overlapping isotopic niches of edge-space foraging and flutter-detecting bats at low and intermediate elevations. Global and regional studies on birds using functional traits demonstrate that niche packing prevails in areas of high productivity such as low elevations and latitudes (Pellissier et al., 2018; Pigot et al., 2016). The only other study comparing isotopic niche partitioning in bat assemblages of low and high species richness found niche packing with high niche overlap in insectivorous bat assemblages across a latitudinal gradient in Africa (Monadjem et al., 2018). Our results are consistent with these observations and also align with previous research using functional traits along the same elevational gradient (Chakravarty et al., 2021). At the presumably resource-scarce high elevation, we found large isotopic niche width with low overlap among functional groups. We suggest that this low niche overlap is an indication of niche partitioning in a potentially resource-deficient, harsh, high-elevation landscape. Similar examples are found in didelphid marsupials and rodents which show low isotopic niche overlap in less productive environments (Bubadu e et al., 2021) or with increased heterospecific competition (Shaner & Ke, 2022).

4.2 | Discordance between functional traits and isotopic niches

Isotopic niche width and overlap at low and high elevation differ from those predicted when using functional traits to varying extents. Chakravarty et al. (2021) found lower than expected (under a null model) functional dispersion at high elevation. Instead, we found large niche width and nearest-neighbour distances at high elevation. This is further backed by the low level of niche overlap among functional groups at this elevation. The reason behind the large nearest-neighbour distance is the dropping off of the redundant flutter-detecting group at high elevation. Rhinolophids that

make up the flutter-detecting group are well-known for having large differences in morphological and echolocation traits that are frequently linked to niche partitioning in the literature (Chakravarty et al., 2021; Voigt et al., 2010). Chakravarty et al. (2021) also attributed the high functional diversity at low elevation to the presence of rhinolophid bats with extreme functional trait values that are drastically different from those of edge-space foraging bats. However, our results place them within the large central hub of the assemblage niche space, as defined by isotopes. This is not surprising as rhinolophid bats have echolocation calls that are adapted to detecting acoustic glints from fluttering insects like Lepidoptera (Tian & Schnitzler, 1997) which also feature in the diet of most aerial foraging bats (Alberdi et al., 2020). The isotopic niche redundancy of this functional group highlights a major discordance in comparison to groups classified using functional traits.

High elevation animal assemblages are often functionally underdispersed (i.e. show homogenous functional traits), a condition referred to as 'environmental filtering' (Chakravarty et al., 2021; de Carvalho et al., 2019; Jarzyna et al., 2020; Montano-Centellas et al., 2020; Reardon & Schoeman, 2017). Our results demonstrate that niche partitioning can occur along other axes (for example, diet and habitat use) even with the homogenisation of functional traits ('environmental filtering'). Similarly, even if biotic interactions limit the similarity of functional traits ('limiting similarity') related to prey acquisition at productive low elevation sites, the actual isotopic or dietary niches may not get delimited (as shown by the high isotopic niche overlap between edge-space and fluttering detecting bats). Using stable isotopes, we detect strong evidence of niche partitioning among functionally similar species.

There is a lack of consensus between the association of species functional traits and their isotopic (or realised) niches. In temperate marine benthic consumers, traits and isotopic niches may be decoupled (Włodarska-Kowalczyk et al., 2019) but they are correlated in freshwater fish assemblages (Fitzgerald et al., 2017). Spider functional groups separate out in the isotopic niche space indicating a match between functional traits and isotopic niches (Sanders et al., 2015). However, as the diet of many rhinolophid bats is well-known, we advise caution against using their morphological and echolocation call measurements to predict trophic niche partitioning with other functional groups.

4.3 | Insights on the diets of poorly known bat species

We uncovered interesting insights on the probable diets of some bat species that have rarely been studied in the wild. As predicted, we observed that trawling bats occupy a peripheral niche space. However, contrary to our predictions, they had the largest niche width (along with edge-space foraging and active-gleaning bats). This functional group consisting of only one species, *Myotis longipes*, is exclusive to low elevation. *M. longipes* is morphologically adapted (large feet and plagiopatagium attached to the ankles instead of toes)

to hunt insects by trawling the surface of water with its feet (Bates & Harrison, 1997; Chakravarty et al., 2020; Morales et al., 2019). Animals that have diets of aquatic origin typically show depleted (more negative) $\delta^{13}\text{C}$ values (Oelbaum et al., 2019; Voigt et al., 2015), but this idea is not supported by our data as *M. longipes* has the highest $\delta^{13}\text{C}$ values in our community. They also forage over a wide range of trophic levels (high range of $\delta^{15}\text{N}$ values), including at high trophic levels, and show low overlap with other functional groups. European trawling species also seem to forage at higher trophic levels than other functional groups (Voigt et al., 2015). Our data suggest that active gleaning bats forage in aquatic environments which deviates from what is known about the species in this functional group. *Murina* spp. that constitute the active foraging group have short, broadband calls that are thought to be an adaptation for navigating in dense forest and in gleaning arthropods like spiders (Kingston et al., 1999). Evidence for spider consumption is based on morphological identification of prey remains but molecular diet analysis of two sympatric *Murina* spp. from Japan suggest that they predominantly prey on lepidopterans and dipterans (Heim et al., 2021). In our study area, *Murina* spp. seem to feed on insects belonging to the lowest trophic levels.

Perhaps the most important result is the specialisation in the passive gleaning forager group that is dominated by two species of *Plecotus*, one of which (*P. wardi*) only occurs above 2700m in our study area. *Plecotus* spp. hunt using both aerial hawking and gleaning (Dietz & Kiefer, 2014) and molecular diet analysis of two widespread European species show that they are generalists but with strong selection for noctuid moths (Andriollo et al., 2021; Razgour et al., 2011). Indeed, a study on moth diversity in western Himalayas shows that noctuid moths are more diverse and common than other moth families in the 2900–3400m range (Sanyal, 2015). The restricted elevational distribution coupled with the isotopic specialisation of *P. wardi* make it an important conservation target. Thorough sampling of source (prey and primary producers) and subsequent use of isotopic mixing models will allow us to better identify the diets of our study species. This was beyond the scope of the present study.

4.4 | Conclusions and future directions

The association between niche expansion and packing with increasing species richness has for long fascinated ecologists and biogeographers. Our study is among the very few to employ stable isotope analysis in investigating niche partitioning in animal communities across elevational gradients. This field is conventionally dominated by a trait-based approach. We uncover niche packing in the lowest elevation site. At the highest elevation, the niche width was large, and the overlap among the constituent functional groups was low. Essentially, our results are consistent with studies on bats in Africa (Monadjem et al., 2018) and passerine birds in the Andes where increases in species richness are explained by niche packing (Pigot et al., 2016). We also detect discrepancies between inferences made using functional traits and a finer measure of niche

using stable isotopes. High elevation animal assemblages are often functionally similar which is inferred as the lack of niche partitioning. However, we show that even functionally similar species/functional groups partition their niches in harsh environmental conditions. We highlight the additional insights offered by combining functional trait analyses with stable isotope information as a proxy for dietary niches. Future studies may focus on investigating niche partitioning between species within each functional group, and on investigating the role of intraspecific vs inter-specific niche partitioning in influencing patterns of niche packing and expansion.

AUTHOR CONTRIBUTIONS

Rohit Chakravarty, Viktoriia Radchuk and Christian C. Voigt conceived the ideas and generated funds; Rohit Chakravarty conducted fieldwork; Christian C. Voigt and Shreyas Managave funded the lab work, and lab data were generated by Rohit Chakravarty and Shreyas Managave; Rohit Chakravarty and Viktoriia Radchuk analysed the data; Christian C. Voigt and Viktoriia Radchuk supervised the research; Rohit Chakravarty led the writing with inputs from all co-authors. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.44j0zpcjc> (Chakravarty et al., 2023).

ORCID

Rohit Chakravarty  <https://orcid.org/0000-0001-7432-6917>
 Viktoriia Radchuk  <https://orcid.org/0000-0003-3072-0095>
 Shreyas Managave  <https://orcid.org/0000-0003-3275-1936>
 Christian C. Voigt  <https://orcid.org/0000-0002-0706-3974>

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SUPPORTING INFORMATION

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

Figure S1: Dispersion in ^{13}C and ^{15}N values of plant samples collected across the elevational gradient (Green crosses: low elevation, red triangles: intermediate elevation, and black dots: high elevation).

Figure S2: Dispersion of ^{13}C and ^{15}N values in insect samples collected across the elevational gradient (Green crosses: low elevation, red triangles: intermediate elevation, and black dots: high elevation).

Figure S3: Changes in niche width of functional groups across elevations when the sample size is reduced to four individuals per functional group per elevation.

Figure S4: Niche overlap probability of guild A (row) being in the dietary niche of guild B (column), calculated at the level of the assemblage.

Table S1: Mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of plant samples collected across elevations.

Table S2: Niche overlap probabilities for guilds at low elevation

Table S3: Mean niche overlap probabilities for guilds at intermediate elevation.

Table S4: Mean niche overlap probabilities for guilds at high elevation.

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