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Turnover in butterfly communities and traits along an elevational gradient in the eastern Himalaya, India

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Abstract

Beta (β)-diversity varies along environmental gradients, and understanding what drives such variation might provide insights into the factors that shape community structure from place to place. Here, we delineate the spatial pattern of β-diversity, analyze its underlying mechanisms, and examine variation in functional traits of butterflies along an extensive elevational gradient (300–3000 m) in the eastern Himalaya, the largest mountain system in the world. We sampled butterflies at 16 sites along this gradient using a fixed-width point count method and estimated habitat variables at each site. We obtained trait data from our field collections and secondary sources as necessary. We partitioned β-diversity into its turnover, nestedness, balanced variation, and abundance gradient components. We used generalized dissimilarity modeling to determine the underlying mechanisms affecting the pattern of β-diversity along the gradient. The pattern of β-diversity in butterflies at adjacent sites exhibited a mid elevation peak. Dissimilarity between sites increased with the increase in distance between the sites. Turnover or the balanced variation made major contributions to the overall β-diversity. Among the set of factors, actual evapotranspiration was positively correlated with β-diversity. The trait-based analysis revealed biogeographic affinity as the best predictor of community composition along the elevational gradient. The high β-diversity arises from turnover rather than nestedness component. We conclude that the pattern of β-diversity of butterflies in the Himalaya is largely due to environmental filtering rather than geographic extent.

KEYWORDS
beta-diversity, butterflies, elevation gradient, environmental filtering, generalized dissimilarity model, nestedness, trait composition, turnover

INTRODUCTION

Over the past few decades, there has been a near constant effort to understand variation in biological diversity across spatial and environmental gradients. However, many of the studies have focused on determining the patterns of species richness at local (α-diversity) or larger scales (γ-diversity) (Fleishman et al., 2005; McCain &

Grytnes, 2010; Rana et al., 2019). Beta (β)-diversity is generally defined as variation in the composition of species among sites (Anderson et al., 2011) and provides the link between α-diversity at local scales and γ-diversity at more regional scales. β-diversity might also vary along the spatial gradients (Anderson et al., 2011; Whittaker, 1960), and understanding what drives such variation could provide insights into the factors that shape community structure (Kraft et al., 2011), patterns of α-diversity across sites (da Silva et al., 2018), or help formulate landscape-level conservation strategies by identifying areas that should be prioritized for conservation (Gomes et al., 2020). One of the key methods to quantify the variation in species composition is to partition β-diversity into its turnover and nestedness components (Baselga, 2010, 2013). The turnover component of β-diversity reflects the phenomenon of species replacement by other species from site to site as a result of environmental sorting or temporal and spatial constraint (Qian et al., 2005). Nestedness, in contrast, occurs when species-poor assemblages are subsets of more species-rich assemblages as a result of nonrandom processes such as colonization and extinction along the gradient. Therefore, partitioning the two components is necessary to elucidate the underlying mechanisms that shape variation in the composition of communities along gradients (Baselga, 2010).

Variation in community composition along spatial gradients may arise because of niche differences among species in the regional species pool (Legendre et al., 2005; Whittaker, 1956). Such a niche-based view would posit that landscapes are mosaics with distinct environmental characteristics, and the environment assembles communities by filtering species based on their niches or traits. Thus, sites that share similar environmental conditions should harbor fairly similar communities. An alternative view suggests that the variation in community composition is created from the dispersal limitation and demographic fluctuations due to events such as colonization, speciation, or extinction (Bell, 2001; Hubbell, 2001; Legendre et al., 2005; Qian et al., 2005; Tuomisto et al., 2003). There is a general consensus that both environmental sorting and dispersal limitation work in concert to assemble ecological communities (da Silva et al., 2018; Leibold et al., 2004); however, the relative importance of each may vary across scales, taxa, and regions (Laliberté et al., 2009; Soininen et al., 2018).

Traditionally, metrics based on taxonomic composition have been used to assess patterns of β-diversity, while functional similarities between the communities were largely ignored (but see Fukami et al., 2005; Kraft et al., 2008; Swenson et al., 2011). Since the expression of traits (both within and among species) changes as environmental conditions change (Cornwell & Ackerly, 2009; Read et al., 2014), information on traits can help uncover mechanisms driving community assembly that may be missed by using only taxonomic β-diversity indices (McGill et al., 2006; Siefert et al., 2013). For example, when environmental conditions between two or more sites differ, one set of species may be replaced by another set because of environmental filtering of species based on their traits (Siefert et al., 2013; Swenson et al., 2011). In contrast, when environmental conditions are similar between two sites, ecological communities may still show high species turnover but share similar functional trait composition (Dehling et al., 2020; Qian & Ricklefs, 2000). In such cases, dispersal limitation and geographic distance result in dissimilarity of the two communities. Therefore, it is imperative to understand trade-offs between species composition and functional trait composition in order to develop a more robust framework of β-diversity patterns along spatial gradients.

Mountain regions are home to much of the world's terrestrial biodiversity (Spehn et al., 2010). Due to a typically systematic variation in climate with elevation, the distribution of biodiversity in mountains also varies, sometimes systematically and other times not (McCain & Grytnes, 2010; Rahbek et al., 2019). It is well known that β-diversity between two sites increases with the increase in distance between sites (distance-decay) (Bishop et al., 2015; Wang et al., 2012). However, along the elevational gradients, β-diversity may exhibit midelevational peaks (Acharya & Vijayan, 2015; Levanoni et al., 2011; Naud et al., 2019), increase with elevation (Castro et al., 2019), or display a decreasing trend (Fontana et al., 2020). Variation in niche breadth and mobility of different taxa and local abiotic factors may be responsible for contrasting patterns in β-diversity along the elevational gradient (Fontana et al., 2020). Despite such variation in β-diversity patterns, it is generally accepted that turnover due to environmental filtering is a major cause of variation in community composition along elevational gradients because of abrupt environmental changes (Fontana et al., 2020; Jiang et al., 2019; Kaltsas et al., 2018; Machac et al., 2011). However, a few studies have also found nested structure in community composition along elevational gradients (Patterson et al., 1996; Presley et al., 2012). Currently, there is no general consensus on whether the patterns and processes of β-diversity are consistent among mountain regions, or taxa, around the globe.

Due to the steep elevational gradient, the Himalayan region is a natural laboratory to test biogeographical hypotheses. In recent years, there has been an upsurge in biogeographical studies of multiple taxa, including butterflies, in various parts of the Himalaya (Acharya, Chettri, & Vijayan, 2011; Acharya, Sanders, et al., 2011; Acharya & Vijayan, 2015, 2017; Bhardwaj et al., 2012; Dewan et al., 2021; Rana et al., 2019). In the Himalayan region, species richness of butterflies declines with increasing elevation (Acharya & Vijayan, 2015; Bhardwaj et al., 2012) including in our own study in the Rangeet Valley, eastern Himalaya (see Dewan et al., 2021). In that study, we found a significant influence of actual evapotranspiration and a suite of habitat variables in shaping the α-diversity patterns (Dewan et al., 2021). To date, however, we know little about patterns in β-diversity and trait variation in butterflies, despite their ability to uncover mechanisms of community assembly (but see Tonkin et al., 2017; Hu et al., 2018).

In this study, we assess community composition (β-diversity patterns) of butterflies along the elevational gradient in Rangeet Valley, Sikkim, eastern Himalaya. We analyzed β-diversity at two levels: (1) stepwise β-diversity of adjacent elevational zones along the elevational gradient and (2) pairwise β-diversity along the gradient (starting from the lowest elevational zone with all other elevational zones, and the next zone with all other zones and so on). Since butterflies depend exclusively on plants for their entire life cycle and closely track plant species richness and density (Acharya & Vijayan, 2015; Sharma et al., 2020), we hypothesized that β-diversity would peak at midelevations coinciding with the zone of maximum transition in vegetation parameters. For pairwise β-diversity, we predict that β-diversity will increase with increasing elevational distance. We partitioned β-diversity into its additive components for both incidence-based (turnover and nestedness) and abundance-based (balance variation and abundance gradient) indices. We predicted that the β-diversity would be mainly driven by the turnover component because elevational turnover patterns are commonly observed in terrestrial invertebrates (Bishop et al., 2015). We also determined the processes that influence the pattern of β-diversity in butterflies along the elevational gradient. We asked whether niche-based processes (e.g., environmental filtering) or more neutral process (i.e., dispersal limitation) are the major determinants of the elevational β-diversity pattern of butterflies. We then analyzed the importance of individual variables in shaping the community composition of butterflies along the elevational gradient.

Lastly, we analyze the effect of environmental factors along the elevational gradient on trait composition of butterfly assemblages. The traits are important aspects of butterfly ecology and thus influence the community assemblage mechanism in the mountains. We use traits such as dietary specialization, elevational range size, wingspan, and biogeographic affinity that encompass important aspects of butterfly ecology such as feeding strategies, dispersal capabilities, and environmental tolerances (Barbaro & van Halder, 2009; Kaltsas et al., 2018; Leingärtner et al., 2014). We hypothesize that these butterfly traits also show variation along the elevation in the Himalaya. We predict that similar environmental condition would favor assemblages of butterflies with similar traits. We then linked species composition and traits of butterflies with the environmental factors along the elevation. To our knowledge, this is the first attempt to understand trait-based assemblages of butterflies along an elevational gradient in the Himalaya.

MATERIALS AND METHODS

Study area

We conducted this study in Sikkim, which is one of the mountain states in northeast India, and part of the Himalaya biodiversity hotspot. The Himalaya forms the highest and longest mountain chain system in the world and can be divided geographically into western, central, and eastern Himalaya. The study sites were located in the Rangeet valley, which spans the south and west districts of Sikkim in the eastern Himalaya (Figure 1, Appendix S1: Figure S1). The elevation of the valley ranges from 300 m in the lowland tropical areas to 8586 m (summit of Mt. Khangchendzonga, third highest mountain in the world). The lower valleys experience hot and humid climate, while the highland areas are cold with very little moisture almost throughout the year. The continuous gradation of elevation and associated climate influences the assemblage and distribution pattern of flora and fauna in this mountain landscape. The vegetation types prevailing in this region transition at approximately every 900 m elevation (Appendix S1: Figure S2; Acharya & Sharma, 2013; Haribal, 1992). For our study, we selected a total elevational range of 3000 m (300–3300 m) because sampling in the high-elevation area (>3300 m) was logistically not viable, and besides, only a few species of butterflies are expected above this elevation (see Acharya & Vijayan, 2015) due to the extreme climatic conditions.

Butterfly sampling

We used fixed points marked along permanent transects to sample butterflies following Acharya and Vijayan (2015). While the Pollard walk method is considered the best technique to sample butterflies, this method requires one to walk at a steady pace along the transects while sampling butterflies in an imaginary 5-m^3 box plot (Pollard, 1977). It is difficult to walk steadily in a rugged, sloping, and slippery terrain; hence, fixed points set along nonlinear transects are more feasible in mountainous landscapes. This method has been recognized as one of

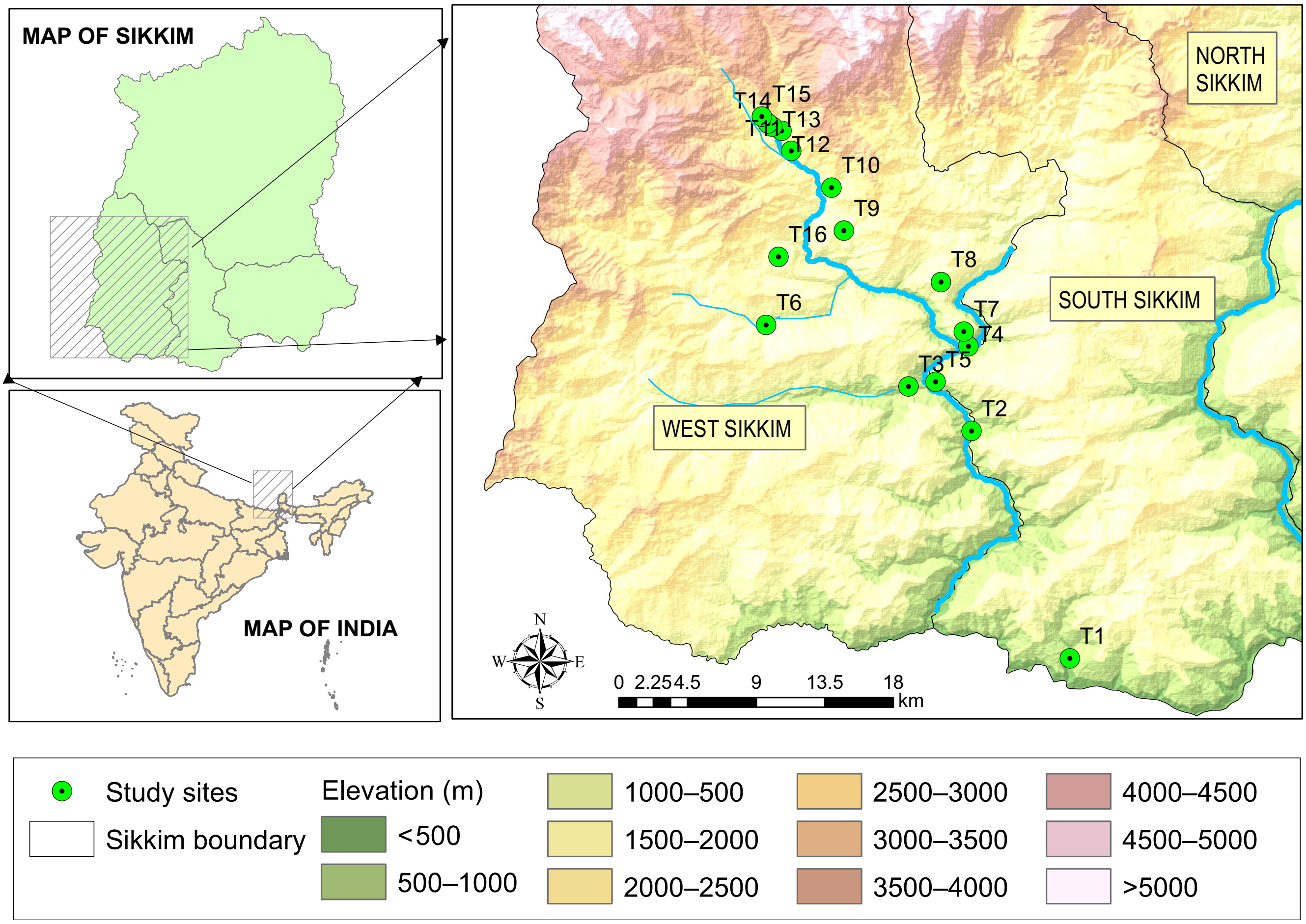

FIGURE 1 Map showing the sampling sites along the elevation gradient in Rangeet Valley, Sikkim, eastern Himalaya

the best techniques to sample butterflies in the mountains (Kral et al., 2018) and has been frequently used in previous studies (Acharya & Vijayan, 2015; Sharma et al., 2020). We divided the total elevational range (3000 m) into 16 vertical elevational zones of 150–200 m width. In each zone, suitable forest sites were selected based on their accessibility and the feasibility of sampling butterflies (Figure 1). We selected natural forest trails, which were free from human disturbances. A transect of approximately 1000 m length was established in each of the 16 elevational zones, and 10 permanent points were marked along each transect. In order to avoid recounting of the same individual butterflies during sampling, a distance of at least 100 m was maintained between the points. For 5 minutes, we recorded butterflies within a radius of 5 m from the center of each permanent point. Sampling was conducted only on clear sunny days from 10:00 AM to 1:00 PM when butterflies are most active. We used Haribal (1992) and Kehimkar (2016) to identify butterflies on the wing. Those butterflies, which could not be identified in the field, were photographed and later identified by referring to guidebooks and ifoundbutterflies.org (Kunte et al., 2019). Since butterflies are highly seasonal, we covered the three main seasons in a 2-year period (2016–2018); premonsoon (March–May), monsoon (June–August), and postmonsoon (September–November). Butterfly sampling in each transect was replicated three to four times in all the seasons.

Traits and species groupings

We selected four butterfly traits—range size, wingspan, larval host-plant specialization, and biogeographic affinity—which are known to be good predictors of species response to elevation (Appendix S2: Table S1; Kaltsas et al., 2018; Leingärtner et al., 2014). Range size is the difference between the highest and lowest elevations where the butterflies were recorded. We added 100 m (50 m at both lower and upper bounds) to the range of the butterflies and assume the species to be present throughout this range (Stevens, 1992). Adding the ranges ensures that species recorded at only one elevational site would have at least the range of 100 m, which otherwise would have the observed range of 0 m. The range augmentation will not affect the species composition along the elevation as the added range does not extend to other adjacent elevational zones (the elevational distance between two consecutive zones is 150–200 m). Data on wingspan of the butterflies were obtained from Kehimkar (2016). We assigned biogeographic affinity to the butterfly species following Holloway (1974) into (1) global, (2) oriental, (3) Palearctic, and (4) afro-tropical species. Information on host plants of the butterflies was collected from the literature (Haribal, 1992) supplemented by field observations. We categorized butterflies as (1) monophagous, (2) oligophagous, and (3) polyphagous species (Dewan et al., 2021; Zhang et al., 2019). Information on host-plant specialization and biogeographic affinity was missing for a few species. In such cases, data from the genus level were extrapolated to species level following Gunton et al. (2011) and Leingärtner et al. (2014). The method assumes that the traits are phylogenetically conserved to some degrees at least in the taxonomic (genus) level considered (Kissling et al., 2014).

Predictor variables

We assessed several environmental variables that potentially influence the species composition of butterflies. As a habitat variable, we estimated richness and density of trees and shrubs along the same transects established for sampling butterflies. To sample trees, we placed 10 × 10 m quadrats in the same spots where permanent points for butterflies were earlier laid. For quantification of shrubs, two smaller quadrats of 5 × 5 m were placed diagonally within each of the 10 × 10 m quadrats. Hence, 10 large and 20 small quadrats were enumerated along each of the transects in all the elevational zones. We considered plants with girth at breast height ≥20 cm as trees. We pooled the richness and density of trees and shrubs from all the quadrats to transect level for each elevational zone.

We used Normalized Difference in Vegetation Index (NDVI) as a surrogate for aboveground primary productivity (Nieto et al., 2015). We first obtained 3 years (2016–2018) of Landsat 8 imagery of the Sikkim Himalayan region (available at 30 m resolution; downloaded from http://earthexplorer.usgs.gov) for NDVI estimation. We then calculated NDVI in each elevation zone from Near-infrared and Red bands of the Landsat 8 dataset using the formula: NDVI = (Near-infrared − Red)/(Near-infrared + Red) using ArcGIS 10.4. Calculating the NDVI by averaging entire elevation zone may be biased as human habitation areas are also present in those zones. Therefore, we extracted the averaged NDVI of a center pixel and eight adjacent pixels from the raster containing the NDVI values. The center pixel in the raster falls exactly in the midpoint of a transect (1 km long) established for sampling butterflies. Taking the averaged NDVI from nine pixels ensures that values from all the points along the transects are represented.

We used mean annual precipitation (MAP) and mean annual temperature (MAT) from the CHELSA (*Climatologist at high resolution for the earth's land surface areas*) dataset available at a resolution of 30 arc seconds (1-km^2 grid) (Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, & Kessler, 2017; Karger, Conrad, Böhner, Kawohl, Kreft, Soria-Auza, Zimmermann, et al., 2017). We obtained the averaged values of temperature and precipitation for consecutive elevation zones using ArcGIS 10.4. We estimated annual actual evapotranspiration (AET) as a measure of water energy and annual potential evapotranspiration (PET) as a measure of ambient energy (Hawkins & Porter, 2003a) based on MAT and MAP datasets following Kluge et al. (2006) and Acharya, Sanders, et al. (2011).

Data analysis

Assessment of the completeness of sampling effort

We first aggregated our point count data to transect level for each of the elevational zones, and subsequent analyses were done at the transect level (which also represents one elevation zone). We then assessed the completeness of sampling effort invested in the field during the study. In addition to observed species, we quantified estimated and rarefied richness for each elevational zone using the EstimateS software (Colwell & Elsensohn, 2014). Chao 1 and Jackknife 1 were used to estimate richness due to their high precision (Hortal et al., 2006). Sample-based rarefied richness was considered as the number of species rarefied to the lowest number of counts conducted for any site (110 point counts in this case). Species accumulation curves were generated using these estimators to assess the completeness of the sampling effort.

Determining the elevational β-diversity pattern

To estimate β-diversity, we used both incidence-based and abundance-based dissimilarity measures (Baselga, 2010). The total pairwise incidence-based β-diversity was calculated as the Sorenson dissimilarly index (β_{sor}). We then partitioned it into turnover (β_{sim}) and nestedness (β_{nes}) components. The incidence-based dissimilarity measure does not take abundances into account, and hence, rare species will generally be treated similarly to common species. Further, bias correction and variation estimation are impossible with only incidence-based data (see Chao et al., 2006). Therefore, to compensate for biases that may occur in incidence-based estimates of β-diversity, we also calculated abundance-based β-diversity. The total abundance-based β-diversity was calculated as a Bray-Curtis dissimilarity index (d_{BC}) and then partitioned into balanced variation ($d_{BC\text{-}bal}$) and abundance gradient components ($d_{BC\text{-}gra}$) (Baselga, 2013). The balanced variation ($d_{BC\text{-}bal}$) is equivalent to the turnover component, in which individuals of one species are substituted by the same number of individuals but of other species from site to site. The abundance gradient, on the other hand, complements the nestedness component and is caused by individuals being lost from one site to another without the species being replaced. Following Wang et al. (2012) and Fontana et al. (2020), we analyzed β-diversity (and its components) at two levels: (1) stepwise β-diversity that compares one elevational zone with its adjacent elevational zone along the elevation gradient (e.g., 350:500, 500:650, and 650:800 m) and (2) pairwise elevation β-diversity that compares each elevation (starting from the lowest elevation and sequentially all elevation sites) to all other elevations (e.g., 350:500, 350:650, 350:800, 500:650, and 500:800 m). The first method allows us to detect major transitions in the butterfly community along the elevational gradient. Since stepwise β-diversity aids in understanding the pattern along the elevational gradient, we examined how these patterns of β-diversity relate to elevation using both linear and quadratic regression models. The pairwise comparison approach provides insights into distance decay of dissimilarity in butterfly communities with increasing elevational distance. We plotted pairwise dissimilarity values between each elevational zone against elevational distance between the same pair of zones. Prior to this analysis, an elevational distance matrix was created using Euclidean distance. We tested for correlation in overall dissimilarity and its components with the elevational distance using Pearson's correlation test and tested for its significance using a Mantel test. This analysis was conducted using *vegan* (Oksanen et al., 2016) and *betapart* (Baselga & Orme, 2012) packages in R software (R Development Core Team, 2018). We also conducted hierarchical cluster analysis and generated a dendrogram plot using β_{sor} and d_{BC} dissimilarity values of each elevational zone with the function "*hclust*" with the default of complete linkage algorithm in R. In order to test the goodness of fit of the hierarchical clusters, we calculated the cophenetic correlation coefficient (CPCC) that represents correlation between the actual distance and the predicted distances based on a particular hierarchical configuration. The clusters are considered to be fit when CPCC value lies close to 1 and usually above 0.75.

Determining the effect of spatial and environmental variables

In order to understand how space and environment affect the compositional dissimilarities of butterflies along the elevational gradient, we used generalized dissimilarity modeling (GDM). The GDM is a linear matrix-based regression that models compositional dissimilarity between pairs of sites as a function of environmental and geographic distance (see Ferrier et al., 2007 for details). GDM compensates for the nonlinearity in ecological datasets, which mainly arises due to (1) a curvilinear relationship between compositional dissimilarity and increasing environmental distance, and (2) rates of compositional turnover along the environmental gradients that are often nonstationary. To account for nonstationarity in the data, the GDM transforms the predictor variables using maximum likelihood and flexible I-splines to provide the best supported relationship between biotic dissimilarities and environmental/geographic distance. Such scaled and combined distance is then transformed using a log link function to account for curvilinearity between the biotic dissimilarity and environmental/geographic dissimilarities. To fit GDMs, we used dissimilarity matrices and site-by-environment matrices, where sites represent each elevational zone. Prior to GDM analysis, we tested for multicollinearity between the predictor variables. Among the set of variables considered, we found high collinearity between MAT, MAP, PET, and AET. We selected AET as the sole environmental predictor for further analysis as it is likely to be the most ecologically relevant variable along with other biotic variables such as tree species richness, tree density, shrub species richness, shrub density, and NDVI. Along with the environmental predictors, we also used geographic coordinates for calculating geographic distance of the sites in each elevational zone. All transects in our study were 1000 m long, and we used the geographic coordinates of the midpoint of each transect. We tested for importance and plotted the I-splines for each predictor variable. Finally, we partitioned the deviance in the GDM following Borcard et al. (1992) to test the relative importance of environmental and geographic variables. We ran GDM using the *gdm* package (Manion et al., 2017) in R.

Assessing trait composition and its relationship to environmental variables

To investigate how environmental variation along the elevational gradient affects butterfly traits, we used a combination of RLQ (Dolédec et al., 1996) and fourth-corner analysis (Legendre et al., 1997). Both methods are based on co-inertia analysis between sets of three matrices: R (site × environment table matrix is a site × species table), L (matrix is a site × species table), and Q (trait data of the species matrix are a species × trait table). Prior to the analysis, we log transformed the environmental variables to compensate for the skewed dataset caused by various traits having different measurements. For species-level data, we used a Hellinger transformation. In this multivariate analysis, at first, separate ordinations were run on R, L, and Q matrices. Then, the Q matrix was related to the R matrix using L as the link. The analysis of the three matrices creates a fourth matrix (environment × traits), which was used to summarize the joint structure of the three matrices (Dray et al., 2014). For ordination of the R matrix (log transformed), we applied principal component analysis (PCA). Since our Q matrix consisted of mixed data, we performed ordination using Hill/Smith PCA. Correspondence analyses were performed on the L matrix. The fourth-corner method is combined to test the hypothesis produced by the RLQ ordinations. The fourth-corner analysis allows a test of significance of the correlation observed in RLQ ordination axes and species traits or environmental variables (Dray et al., 2014). The significance of this correlation was tested using 999 permutations and referring to p values adjusted through the false correction method (Benjamini & Hochberg, 1995). The RLQ fourth-corner analyses were conducted using the package *ade4* (Dray & Dufour, 2007) in R.

RESULTS

Patterns of β-diversity

We recorded a total of 3603 individual butterflies belonging to 253 species from six families during the study. Species accumulation curves for estimated (Chao 1 and Jackknife 1), rarified, and observed richness begin to plateau, reflecting that sampling was almost complete at the majority of the sites. Since estimated (both Chao 1 and Jackknife 1), rarefied, and observed species richness showed high correlation ($r = 0.99$ and $p < 0.01$), we used only observed species richness for further analyses and modeling. The species richness pattern of butterflies (observed as well as estimated) followed a declining trend with elevation (see Dewan et al., 2021 for details).

The mean pairwise dissimilarity for β_{sor} (incidence-based) and d_{BC} (abundance-based) was 0.735 and 0.794, respectively (Table 1). Partitioning β-diversity (incidence-based) returned a higher contribution of β_{sim} (turnover) compared with β_{nes} (nestedness) in the overall β-diversity. Mean β_{sim} and β_{nes} are 0.600 and 0.135, respectively. Similarly, in the case of abundance-based dissimilarity, $d_{BC\text{-}bal}$ (balance variation) with a mean value 0.693 was more dominant than the $d_{BC\text{-}gra}$ with a mean value of 0.101. Stepwise β-diversity between two adjacent elevation sites showed two peaks of species dissimilarity: one between 950 and 1150 m and other between 2100 and 2300 m (Figure 2, Appendix S2: Table S2). The quadratic models, with their lower Akaike information criterion values, performed better than the linear models in explaining the β-diversity pattern along the elevational

TABLE 1 Mean, SD, minimum (Min), and maximum (Max) range of the overall incidence-based (β_{sor}) and abundance-based (d_{BC}) dissimilarities of butterflies and their substitution components observed in Sikkim, eastern Himalaya

Beta diversity indices and their components	Mean	SD	Min	Max
β_{sor}	0.735	0.203	0.043	1.000
β_{sim}	0.600	0.200	0.000	1.000
β_{nes}	0.135	0.072	0.000	0.361
d_{BC}	0.794	0.192	0.014	1.000
$d_{BC\text{-}bal}$	0.693	0.238	0.000	1.000
$d_{BC\text{-}gra}$	0.101	0.095	0.000	0.435

Note: Components of β-diversity: β_{sim}—turnover, β_{nes}—nestedness, $d_{BC\text{-}bal}$—balanced variation, and $d_{BC\text{-}gra}$—abundance gradients.

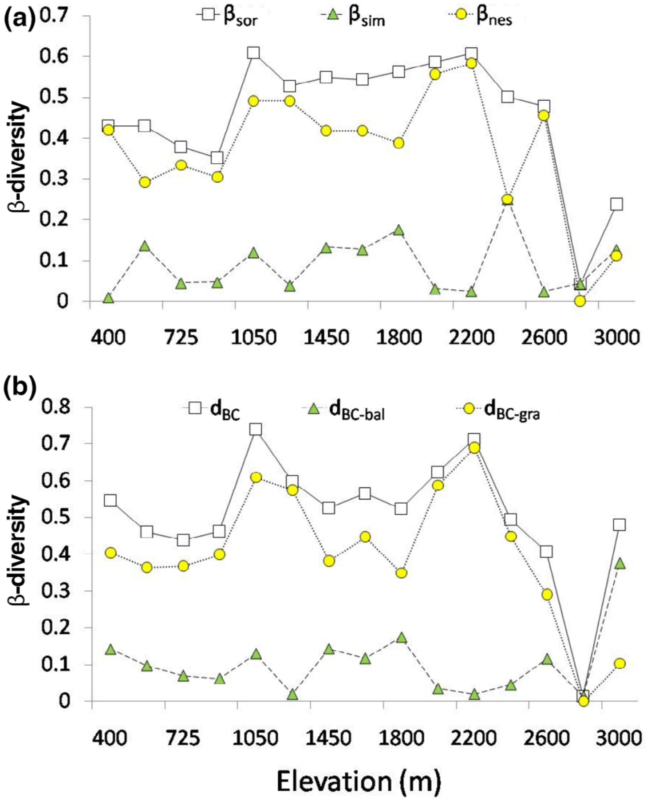

FIGURE 2 Pairwise (a) incidence-based and (b) abundance-based β-diversity of butterflies between two adjacent sites along the elevation gradient in Rangeet Valley, Sikkim, eastern Himalaya. β_{nes}, nestedness; β_{sim}, turnover; β_{sor}, Sorenson dissimilarity index; d_{BC}, Bray-Curtis dissimilarity index; $d_{BC\text{-}bal}$, balanced variation; $d_{BC\text{-}gra}$, abundance gradient

gradient (Appendix S2: Table S3). The models showed a unimodal pattern of β-diversity along the elevational gradient. β_{sor}, β_{sim}, d_{BC}, and $d_{BC\text{-bal}}$ were significantly higher at midelevations than at low or high elevations, following the unimodal pattern. β_{nes} and $d_{BC\text{-gra}}$ did not show any significant pattern with the elevational gradient.

Mantel tests indicated a significant increase in pairwise incidence-based β-diversity, β_{sor} ($r = 0.8226$, $p < 0.01$), β_{sim} ($r = 0.76$, $p < 0.01$), and β_{nes} ($r = 0.21$, $p < 0.05$), with increasing elevational distance between sites (Figure 3). Similarly, the abundance-based β-diversity—d_{BC} ($r = 0.80$, $p < 0.01$) and $d_{BC\text{-bal}}$ ($r = 0.74$, $p < 0.01$)—increased significantly with increasing elevational distance, but $d_{BC\text{-gra}}$ ($r = -0.23$, $p = 0.986$) was not significantly correlated with elevational separation. Cluster analysis based on β_{sor} (CPCC = 0.895) and d_{BC} (CPCC = 0.85) showed a separate cluster for butterfly assemblages of low and midelevations, which was distinct from the high-elevation butterfly communities (Appendix S3: Figure S1).

GDM and deviance partitioning

Based on the generalized dissimilarity model, variation in AET, tree species richness, tree density, and geographic distance between different elevational zones were all significant predictors of β_{sor}. Among all the variables, variation in AET was the most important predictor for β-diversity measures followed by tree richness, tree density, and geographic distance (Table 2, Appendix S3: Figure S2). The full GDM explained 88.03% of the total deviance observed in the model. In the deviance partitioning approach, pure environmental variables alone explained 87.8% of the deviance, while geographic distance explained only 0.001% variation. The combined deviance (explained by environmental variables and geographic distance) was only 0.21%. A similar pattern was found in the case of β_{sim} where a model with AET, tree richness, tree density, and geographic distance had the best fit. The full model explained about 76.8% of the deviance observed in β_{sim}. Here, environmental variables alone explained 76.1% of deviance and geographic distance explained 0.13%, while 0.23% of the total deviance was shared between these two factors. With the β_{nes} model, only AET was a significant predictor. Environmental variables explained 7.39% of the deviance observed in the model, while geographic distance made no contribution.

Similar to the incidence-based β-diversity, variation in AET, tree species richness, tree density, and geographic distance were significant predictors of d_{BC} and $d_{BC\text{-bal}}$

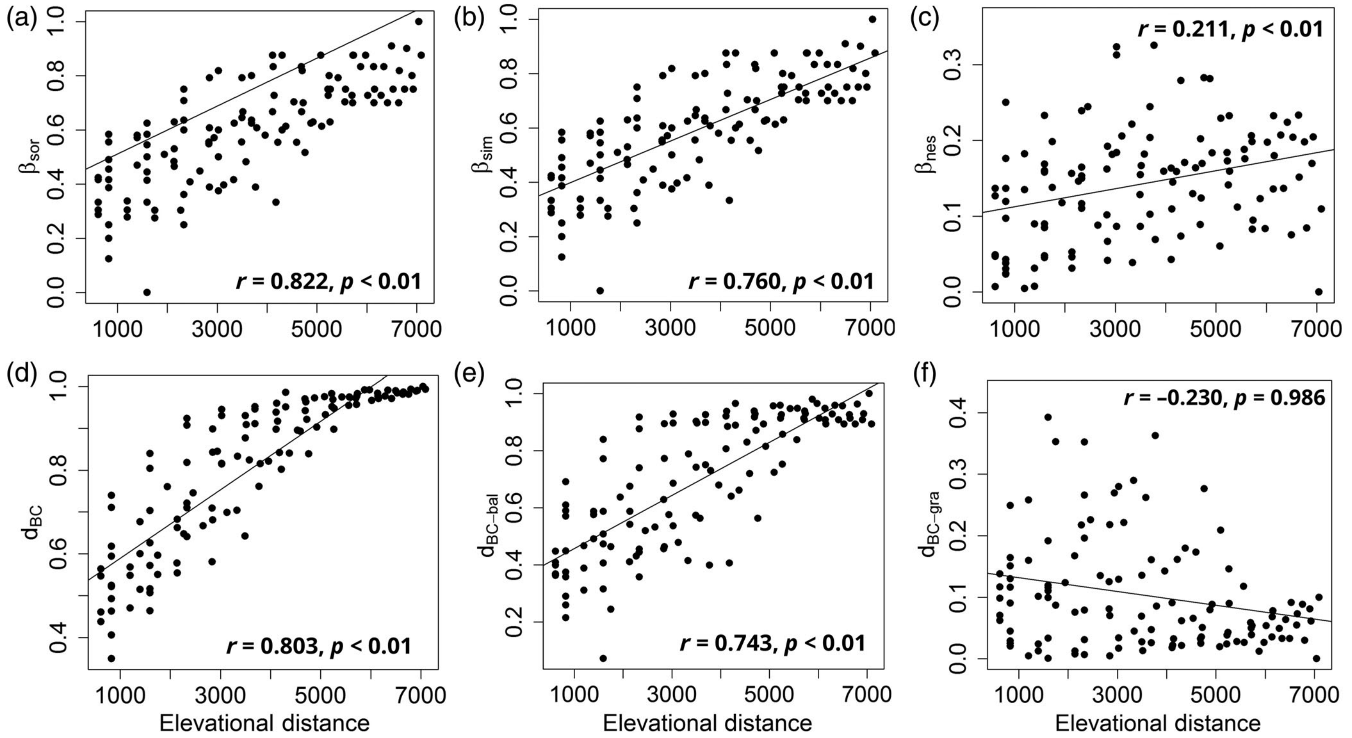

FIGURE 3 Relationship between biotic dissimilarity of butterflies and elevational distance in Rangeet Valley, Sikkim, eastern Himalaya. Biotic dissimilarity is measured as (a) Sorenson dissimilarity index (β_{sor}), (b) its turnover (β_{sim}), and (c) nestedness (β_{nes}) components; (d) Bray-Curtis dissimilarity index (d_{BC}), (e) its balanced variation ($d_{BC\text{-bal}}$), and (f) abundance gradient ($d_{BC\text{-gra}}$) components. Pearson correlation coefficient (r) and significance (p) computed using Mantel tests are also shown

TABLE 2 A summary of generalized dissimilarity models (GDM) showing the relationship between incidence-based (β_{sor}) and abundance-based (d_{BC}) dissimilarities of butterflies in Sikkim, eastern Himalaya, and their additive components with environmental variables and geographic distance

Statistic or variable	β_{sor}	β_{sim}	β_{nes}	d_{BC}	$d_{BC\text{-}bal}$	$d_{BC\text{-}gra}$
Null deviance	26.564	21.452	5.909	27.850	34.136	10.616
GDM deviance	3.179	4.969	5.319	3.419	6.162	9.192
Percentage deviance explained	88.031	76.837	9.982	87.723	81.949	13.412
Intercept	0.000	0.000	0.088	0.000	0.000	0.067
Variable importance						
Geographic	**0.000**	**0.770**	0.000	**0.000**	**0.000**	0.000
TRS	**3.550**	**4.246**	5.063	**5.518**	**9.093**	0.000
TD	**1.837**	**3.991**	0.040	**1.006**	**2.617**	0.000
SSR	0.528	0.810	3.687	0.107	0.215	5.789
SD	0.606	0.802	0.000	**0.845**	0.045	35.837
AET	**46.420**	**43.461**	**46.430**	**40.147**	**35.398**	0.832
NDVI	0.743	0.527	12.157	0.201	0.213	5.829

Note: Significant variables ($p < 0.05$) are marked in bold. Components of β-diversity: β_{sim}—turnover, β_{nes}—nestedness, $d_{BC\text{-}bal}$—balanced variation, and $d_{BC\text{-}gra}$—abundance gradients.

Abbreviations: AET, actual evapotranspiration; NDVI, Normalized Difference in Vegetation Index; SD, shrub density; SSR, shrub species richness; TD, tree density; TRS, tree species richness.

(Table 2, Appendix S3: Figure S3**)**. Among these predictors, AET was the most important predictor followed by tree species richness, tree density, and geographic distance. These variables explained 86.77% and 81.00% of the deviance observed in d_{BC} and $d_{BC\text{-}bal}$, respectively. Environmental variables independently explained 86.65% and geographic distance explained 0.36% of the deviance observed in d_{BC}, while 0.23% was jointly shared (Figure 4). Likewise, environmental variables and geographic distance, respectively, explained 80.81% and 0.11% of the deviance observed in $d_{BC\text{-}bal}$, and 0.08% of the total deviance was jointly shared by the environmental and geographic distance. In contrast, GDM with shrub density and geographic distance was the best fit for $d_{BC\text{-}gra}$. However, these variables explained only 11.62%, which was explained by environmental variables alone as geographic distance did not contribute to the deviance observed in $d_{BC\text{-}gra}$.

Trait composition of butterfly assemblages

RLQ analysis indicated the overall significant association between butterfly traits and environmental variables (Monte Carlo permutation test; $n = 49{,}999$; $p < 0.05$). The RLQ plots showed the influence of elevation in both taxonomic and trait assemblages. The first two axes of the RLQ projected 98.51% of the total variance (Table 3). The combined RLQ and fourth-corner method showed significant negative associations between environmental variables such as AET, tree density, and tree species richness with the first axis (Table 4, Figure 5). The first axis represented changes in the environmental gradient from a warm and humid tropical landscape at lower elevations to harsh and dry environments at higher elevations. It is also related to the reduction of tree richness and density at higher elevations. Among the traits analyzed, butterflies with a Palearctic affinity were positively correlated with the first axis, but no other butterfly traits showed any significant correlation with any of the other axes.

DISCUSSION

Pattern of β-diversity of butterflies along the elevational gradient

We examined the patterns of β-diversity and community-level trait composition of butterflies along an extensive elevational gradient in the eastern Himalaya. We found that trends in incidence-based dissimilarity mirrored the trends observed in abundance-based dissimilarity. Therefore, each one of the measures could be used in a complementary way to explain the trends of β-diversity in the mountains. Pairwise β-diversity of butterflies increased significantly with increasing elevational separation: That is, elevational zones farthest from each other had a maximum dissimilarity in composition of butterflies.

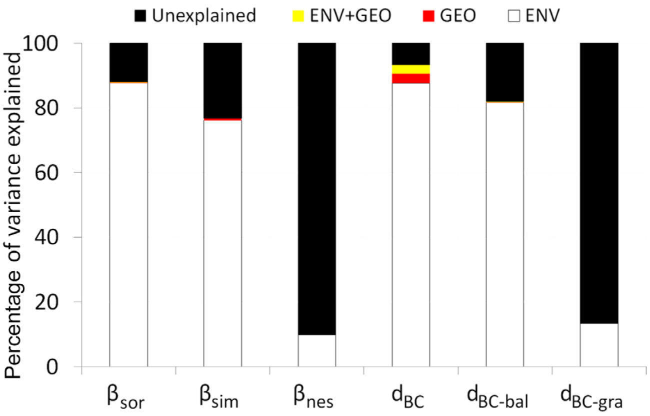

FIGURE 4 Proportion of deviance (shared and independent) of the generalized dissimilarity model explained by the environmental predictors (ENV) and geographic distance (GEO) in explaining Sorenson dissimilarity index (β_{sor}), its turnover (β_{sim}), and nestedness (β_{nes}) components, and Bray-Curtis dissimilarity index (d_{BC}), its balanced variation ($d_{BC\text{-}bal}$), and abundance gradient ($d_{BC\text{-}gra}$) components of butterflies along elevation gradient in Sikkim, eastern Himalaya

TABLE 3 Summary of the RLQ analysis of butterfly traits observed in Sikkim, eastern Himalaya

Statistic	Axis 1	Axis 2
Eigenvalues	0.375	0.073
Correlation	0.372	0.243
Projected inertia (%)	82.412	16.101
Variance retained R (%)	98.218	96.494
Variance retained L (%)	42.094	34.007
Variance retained Q (%)	73.855	76.378

Note: Details of the eigenvalues, correlation, percentage of the total projected inertia explained by the first two axes, percentage variance retained by R (environmental variable matrix), L (species matrix), and Q (species traits matrix) are provided.

Turnover (incidence-based dissimilarity) or the balanced variation (abundance-based dissimilarity) contributed most to the overall β-diversity, indicating that one assemblage of species and its populations were being replaced by different species and populations in other sites (Baselga, 2010, 2013). High substitution of butterfly species along the elevational gradient provides direct evidence that the assemblages in high elevations were not a subset of lower elevations. For instance, only 0.65% of the total species was shared between the lowest (350 m) and the highest elevational zone (3100 m) in our study. High levels of substitution of species and population components indicated that the assemblages of butterflies are relatively exclusive in each of the elevational zones examined here. Therefore, it can be assumed that high regional diversity of butterflies in the Himalaya arises mainly because of rapid turnover among communities. Studies around the world have consistently found a higher contribution of the turnover component in explaining β-diversity patterns for a range of taxa, for example, plants (Zhao et al., 2019), soil Enchytraeidae (Jiang et al., 2019), dung beetles (da Silva et al., 2018), and ants (Flores et al., 2018) along elevational gradient. Similar patterns have also been reported for butterfly communities in eastern Alps, Italy (Fontana et al., 2020), and Olympus and Rhodopes mountain range, Greece (Kaltsas et al., 2018).

While each elevational zone possessed a unique composition of butterflies due to high turnover among elevations, cluster analysis revealed that the butterfly communities could be grouped into three distinct categories: low, mid, and high elevations. Each clusters of the butterfly community was associated with the particular vegetation strictly found in each elevation, for example, low-elevation community to tropical semideciduous forests, midelevation community to subtropical broad-leaved forest, and high-elevation community to temperate broad-leaved forest. Notably, the two elevational peaks in β-diversity lie in the transition zone between these three categories. In our study area, 900–1150 m is chiefly a zone between tropical semi-deciduous forest and subtropical broad-leaved forest (Acharya & Sharma, 2013; Acharya & Vijayan, 2017), which coincides with the peak of β-diversity. Areas between 2100 and 2300 m elevations form another transition zone between subtropical forest and dense temperate broad-leaved forest, and β-diversity also peaked at this elevation. Acharya and Vijayan (2015) have reported a similar midelevational peak in turnover of butterflies from the Teesta Valley of eastern Himalaya, although their peaks occurred at 1650–1850 and 3650–4000 m. High β-diversity between the transition zones is possibly due to the edge effect, which occurs at ecotone boundaries (Despland, 2014). In mountains, the ecotone boundaries separate vegetation zones. Shifts in butterfly assemblages at ecotonal boundaries (or vegetation transition zones) are a commonly observed phenomenon in mountain regions and have been previously reported from northern Chile (Despland et al., 2012) and northern Israel (Kent et al., 2013). Such phenomena are expected in pristine mountain landscapes where abiotic factors associated with elevation filter species into local assemblages, making each elevation zone unique in terms of community composition (Jiang et al., 2019; Kaltsas et al., 2018).

Factors affecting the β-diversity pattern of butterflies along the elevation

Two processes, environmental filtering and spatial constraints, typically influence patterns of β-diversity along

TABLE 4 Combination of fourth-corner and RLQ results showing the relationship between butterfly traits and environmental variables

(a) Butterfly traits	Axis R1	Axis R2	(b) Environmental variables	Axis Q1	Axis Q2
Range size	0.167	−0.116	TRS	**−0.265**	−0.156
Afro-tropical	−0.065	−0.828	TD	**−0.223**	−0.061
Global	−0.046	0.049	SSR	−0.0894	−0.099
Oriental	−0.114	−0.131	SD	−0.188	0.141
Palearctic	**0.272**	0.129	AET	**−0.389**	0.059
Monophagous	0.036	−0.118	NDVI	0.115	−0.124
Oligophagous	0.143	0.001			
Polyphagous	−0.189	0.050			
Wingspan	−0.123	−0.038			

Note: (a) Fourth-corner tests between the first two RLQ axes for environmental variables (AxR1/AxR2) and butterfly traits; (b) fourth-corner tests between the first two RLQ axes for butterfly traits (AxQ1/AxQ2) and environmental variables. Significant association is marked in bold (adjusted $p < 0.05$). Abbreviations: AET, actual evapotranspiration; NDVI, Normalized Difference in Vegetation Index; SD, shrub density; SSR, shrub species richness; TD, tree density; TRS, tree species richness.

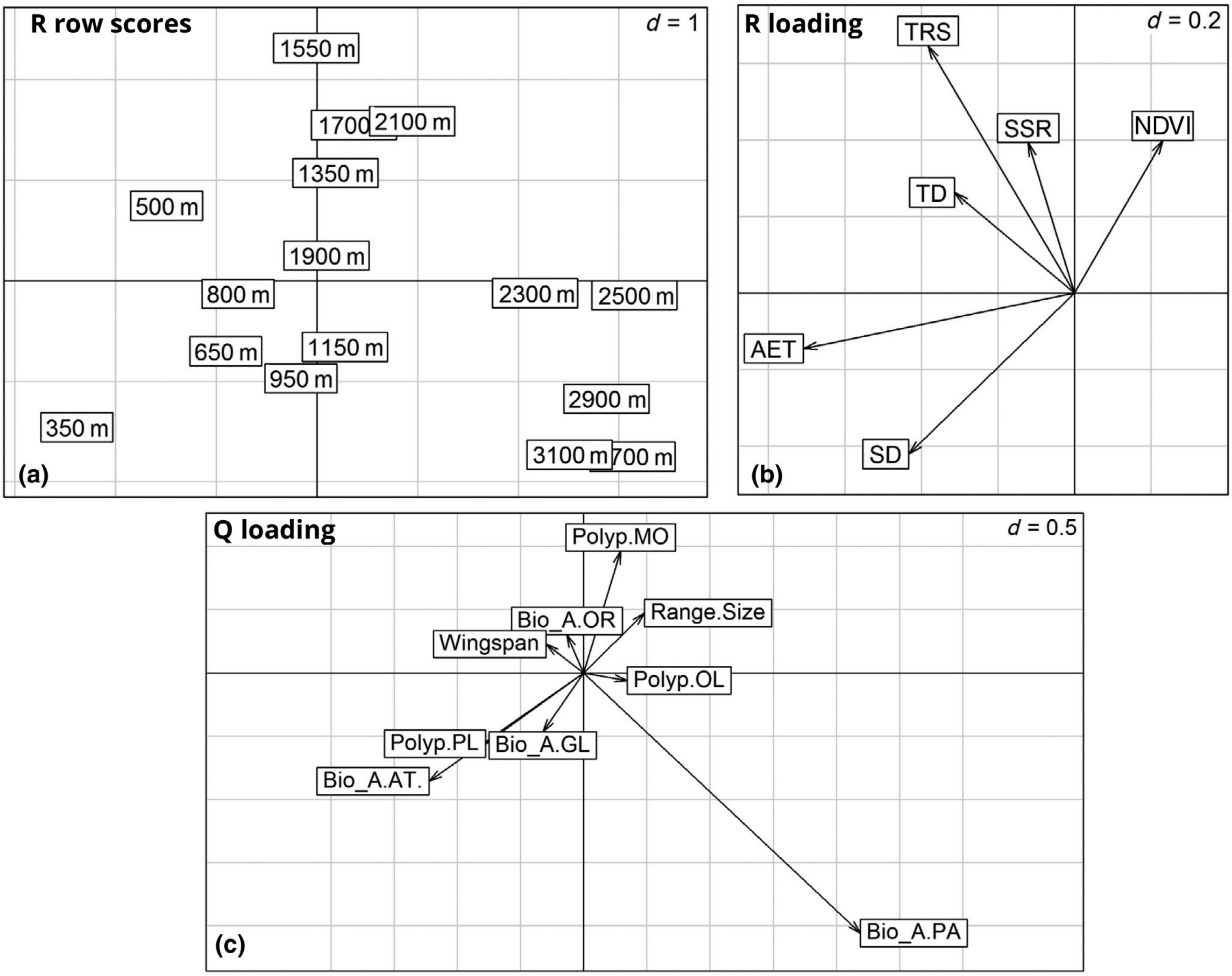

FIGURE 5 Results of RLQ analysis of butterflies showing scores of (a) sites, (b) environmental variables, and (c) traits. (a) Elevation in meters; (b) AET, actual evapotranspiration; NDVI, Normalized Difference in Vegetation Index; SD, shrub density; SSR, shrub species richness; TD, tree density; TRS, tree species richness. (c) Bio_A.AT, afro-tropic species; Bio_A.GL, global species; Bio_A.OR, oriental species; Bio_A.PA, palearctic species; Polyp.MO, monophagous species; Polyp.OL, Oligophagous species; Polyp.PL, polyphagous species

environmental gradients (Legendre et al., 2005; Leibold et al., 2004). Partitioning of the deviance in GDM revealed that a large fraction of deviance in butterfly β-diversity was explained by the environment compared to geographic distance between sites. Based on these findings, we argue that the pattern of β-diversity is largely due to environmental filtering rather than geographic extent. Our finding thus supports the "*niche-based model*" or "*species sorting model*," which relies on the importance of environmental site characteristics in controlling the species composition (Hu et al., 2018; Jiang et al., 2019; Whittaker, 1956) rather than "*neutral processes*" (Bell, 2001; Hubbell, 2001). Inconspicuousness of the effect of geographical distance on β-diversity is probably due to the smaller spatial scale in our study. It is widely accepted that β-diversity depends on the spatial scale (grain size and extent) (Laliberté et al., 2009; Soininen et al., 2018). The aerial distance of entire stretch of Rangeet Valley is approximately 65 km (from the lowest point of the valley to the tip of Mt. Khangchendzonga). Hence, it is less likely that geographic extent (such as in our study) in the region can isolate the dispersal of butterflies. Studies have already proved that environmental filtering is more influential at smaller or regional scale, while spatial constrain (dispersal limitation) may have more profound effect in the larger scale (López-Delgado et al., 2019; Qian & Ricklefs, 2000).

Among the set of environmental variables, variation in AET, tree species richness, and tree density had the largest effect on β-diversity of butterflies. AET directly influences the physiology of an organism (through the effect of temperature/light stress and water availability) and regulates the productivity of an ecosystem (Hawkins & Porter, 2003a). Being ectothermic organisms, butterflies depend largely on regulating temperature as energy for maintaining their physiology, and water availability in all forms (nectars, mud puddles, and fruit juices) is crucial because butterflies are dominantly liquid feeders (Fleishman et al., 2005). It is widely believed that at local levels, the diversity of animals is strongly influenced by the diversity of plants (Acharya & Vijayan, 2017; Haddad et al., 2001; Siemann et al., 1998). Similarly, butterflies are dependent on availability of larval host plants for acclimation to new habitats (Despland, 2014). However, at the regional or broader geographical scale, several studies have demonstrated an association between herbivores and climatic factors rather than plants (Hawkins & Porter, 2003b). Hawkins and Porter (2003b) showed a positive correlation between plants and butterfly distributions at moderate scales, but once the water-energy balance (AET) and topographic variables were added into a regression model, the effect of plants became nonsignificant. Their finding suggests that butterflies and plants respond synchronously to the climatic variation. The ambient climatic conditions (such as AET) facilitate growth of more vegetation by influencing the resources availability for plant growth. AET has been reported to significantly influence the pattern of tree diversity along the elevation in the eastern Himalaya (Acharya, Chettri, & Vijayan, 2011; Rana et al., 2019). Climatic conditions shape the structure and composition of the vegetation types, which, in turn, determine the butterflies that are ultimately adapted to such habitats. Differences in habitat diversity and structure such as plant species richness, understory coverage, canopy openness, and basal area are plausible factors that can influence β-diversity of butterflies in a range of ecosystem types (Sharma et al., 2020). In the eastern Himalaya, AET is known to decrease linearly with elevation leading to a climate–habitat gradient (Trabucco & Zomer, 2010). The synchronous response of vegetation and butterfly community to climate is also reflected through cluster analysis in our datasets as composition of butterfly in different clusters directly corresponds to composition of vegetation found therein. The lower elevations have warmer heterogeneous habitats with high productivity and support a diverse group of butterfly communities. The butterfly communities found in the harsh and less productive highlands are characterized by a few specialist species. Here, the harsh environmental conditions act as a deterministic filter on community assembly of butterflies leading to the selection of only a few species that have evolved specialized traits allowing them to thrive/survive in those niches. Future studies on interaction between vegetation structure and community/trait composition of butterflies along the elevational gradients would provide more insights on β-diversity of butterflies in the mountains.

Trait composition of butterflies along the elevation

Niche or trait differences among assemblages are perhaps largely due to the historical affinities of particular species toward specific biogeographic realms. In the Himalayan region, species occurring at low to midelevations are mostly represented by the oriental elements (Indo-Malayan or Indo-Chinese) adapted to the tropical hot/humid climate, whereas the high-elevation butterfly assemblages are mostly Palearctic species that show wider climatic tolerance and are also adapted to the colder temperate region (Haribal, 1992; Holloway, 1974; Mani, 1974). This phenomenon explains the unique clusters of butterfly community observed in the lower and higher elevation in this study. The biogeographic affinity of butterflies indicates high phylogenetic relatedness; for example, the butterflies of genus *Pieris* or *Argynnis*, which showed high environmental tolerance, had the affinity toward Palearctic realm. The "*tropical niche conservatism hypothesis*" explains that the affinity of butterflies toward tropical environments is an ancient, conserved trait and that evolution of cold tolerance in the new derived taxa (Palearctic species in this case) allows them to colonize colder climatic regimes (DeVries, 2000; Hawkins & DeVries, 2009). "*Vertical colonization*," wherein highlands would be colonized by the elements arising from the lowland lineages as a result of cold environmental adaptation, has also been suggested as a plausible explanation for dung beetle assemblages in the mountains of southern Brazil (da Silva et al., 2018; Lobo & Halffter, 2000). Evidence suggests that some of the oriental clades have expanded their ranges upward toward the highlands: For example, the majority of the butterfly species in the genus *Lethe* are found at low- or mid elevation sites, but a few species such as *Lethe nicetlla* or *Lethe maitrya* inhabit higher elevation areas (2700–3800 m) (Kehimkar, 2016). However, vertical colonization does not apply to a large proportion of the butterfly communities in the Himalaya. Rather, the colonization history of the majority of butterflies is more complex than generally anticipated. Oriental forms originating in the Tertiary mountains east and southeast of India followed their upward and westward movement and began colonizing the lowlands of the newly rising Himalaya between the Pliocene and early Pleistocene (Mani, 1974). The Palearctic fauna that diversified in colder Turkmenistan and Mediterranean subregions appeared in the west of Himalaya in the Pleistocene when the mountains had already formed (at least above timberline). Species were raised to higher elevations with continued orogenic uplift and then radiated out in an eastward direction through high-elevation passes as seen in the butterfly genus *Paranassius* on the Qinghai–Tibetan Plateau (Su et al., 2020). The colonization history of butterflies suggests that the dispersal mechanism is important in shaping the current assemblages of butterflies in the Himalayan landscape.

Other butterfly traits such as dietary specialization and wingspan, and elevational range size did not affect the assemblage pattern of butterflies in this study. The "*altitudinal niche-breadth hypothesis*" explains that the diet breadth of herbivore increases with increasing elevation; that is, more number of species would be polyphagous in the higher elevation, while the lower elevation would be dominated by specialist species (Rasmann et al., 2014). The inconsistency of our results with this hypothesis may be because (1) of scanty information on larval host plants of Himalayan butterflies and (2) the alpine area (>4000 m), which represents a habitat with extreme environment where butterflies with different life history strategies possibly occur, was not considered in this study. Nevertheless, evidence for the hypothesis is also mixed, with some authors showing evidence for the hypothesis (Pellissier et al., 2012), while others show contrasting results (Novotny et al., 2005; Rodríguez-Castañeda et al., 2010). Similarly, we did not find any significant pattern of variation in wingspan of butterfly community along the elevational gradient. Our finding is similar to results obtained for Costa Rican butterflies (Hawkins & DeVries, 1996) and Geometridae moths in the Andean montane rain forest (Brehm & Fiedler, 2004). The elevational patterns in wing size is generally group-specific and therefore shows weak relationship when whole taxa (for instance in this study) are taken into consideration. The elevational range size of butterflies also did not show significant variation among different assemblages along the elevational gradient in this study. The mean elevational range of butterflies does increase with increasing elevation in the eastern Himalaya, indicating that species in the higher elevation generally have higher elevational range than its lowland counterpart (Dewan et al., 2021a, 2021b). However, the elevational range size relationship is weak ($R^2 = 0.538$, $p < 0.01$) and therefore may not be as important as the biogeographic affinity in shaping the assemblages on butterflies along the elevation in the eastern Himalaya.

CONCLUSIONS

We recorded high β-diversity of butterflies in our study along an extensive elevational gradient in the Himalaya, reflecting the importance of the entire gradient for butterfly conservation. Stepwise β-diversity had a unimodal pattern along the elevational gradient coinciding with vegetation transition zones. The β-diversity pattern largely reflected turnover (incidence-based) or balanced variation (abundance-based) components, indicating that assemblages of butterflies were exclusive in each elevational zone along the gradient. We found that the resultant pattern of β-diversity was largely due to environmental filtering rather than geographic extent reflecting the importance of environmental site characteristics in determining the current species composition of butterflies. Similarly, our trait-based analysis suggests that niche division among species was largely due to the biogeographical affinities of butterflies. We opine that current assemblages of butterflies in the Himalaya may also have been influenced by dispersal mechanisms linked to their colonization history. However, more empirical studies covering many elevation gradients across the Himalaya along with phylogeographic assessments would provide a better understanding of the colonization history and current assembly of butterflies in the Himalaya.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Dewan et al., 2021a, 2021b) are available from Figshare: https://doi.org/10.6084/m9.figshare.16608520.

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SUPPORTING INFORMATION

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