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ARTICLE

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Vegetation productivity determines the response of butterflies along elevation gradients in the trans-Himalayas, Nepal

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Abstract

Environmental parameters along elevational gradients affect the number of butterflies and the variety of species. However, which variables play significant roles and how they operate can be difficult to untangle. Here, we examine the relationships between observed butterfly richness (overall and subgroups) at different elevation gradients and remotely sensed environmental variables (vegetation productivity, surface temperature, landscape heterogeneity, and moisture stress) using generalized linear models. We surveyed butterflies with a fixed-point count method in 19 elevation bands within 1600–5200 m above sea level in Manang district, trans-Himalayan region, north-central Nepal. The number of butterflies in each elevation band was studied and estimated, then interpolated across the lowest and highest elevation to estimate butterfly species richness. Then, the selection of models was performed on butterfly richness and elevations to test the best model support based on the lowest value of the Akaike information criterion and a multimodel averaging for other environmental variables. Altogether, 94 butterfly species, representing 20 subfamilies and six families, were recorded throughout the study periods. We obtained cubic model support for overall species richness, Papilionidae, and Hesperiidae, quadratic to Nymphalidae and Pieridae, and the linear model to Lycaenidae. In our study, vegetation productivity was found to have a significant positive impact on butterfly communities. Our study further suggests species richness of Papilionidae and Hesperiidae has a strong positive correlation with surface temperature and landscape heterogeneity and negative associations with moisture stress but other subgroups of butterfly communities including overall species richness showed insignificant relationships with these variables. This study provides significant information related to the responses of montane butterflies to environmental variables along elevational gradients from the Himalayas Nepal. However, further detailed studies on the functional behaviors of butterflies potentially offer more insights into their distribution patterns and ecological relationship in the montane environment.

KEYWORDS
environmental parameters, high altitudes, Manang, spatial scales, species richness

INTRODUCTION

The distribution pattern of biodiversity covaries with several environmental variables (Navarro-Cano et al., 2015) and provides a valuable understanding of the interaction between organisms and environmental gradients (Ashton et al., 2009; McCain & Grytnes, 2010). Numerous studies have explicitly focused on understanding the effects of ecological drivers across altitudinal gradients on biodiversity (Dewan et al., 2022; Fu et al., 2006; Grytnes & Vetaas, 2002; Hodkinson, 2005; Kluge et al., 2006; Körner, 2007; McCain & Grytnes, 2010; Mori et al., 2013; Popović et al., 2021; Viterbi et al., 2013). However, the general pattern and underlying mechanisms of biodiversity across elevational ranges are not understood extensively and are often controversial in spatial ecology (Eisenlohr et al., 2013; Li & Feng, 2015; Peters et al., 2016; Popović et al., 2021; Sanders & Rahbek, 2012). Thus, the study of species diversity patterns along elevational gradients is essential for a systematic understanding of biodiversity dynamics (Ah-Peng et al., 2007; Körner, 2007; McCain, 2007; Sanders & Rahbek, 2012), impact of environmental changes (Dahal et al., 2021; Habel et al., 2021; Kattel, 2022; Thom et al., 2017), species ecological specialization (Stefanescu et al., 2011) and development of effective biodiversity conservation strategies (Gavin & Stepp, 2014; Hunter & Yonzon, 1993; Mtui et al., 2022; Siddig et al., 2016; Vetaas & Grytnes, 2002).

The Himalayas are characterized by an extensive spectrum of physical environments with diverse ecological gradients, and the region constitutes varied climatic conditions across elevation gradients (Bhattacharjee et al., 2017; Ehl et al., 2019). Such variations in the mountain environments have favored unique compositions of biodiversity, ecosystems, and contain a large number of native and threatened species (Acharya et al., 2011; Betz et al., 2020; Catalan et al., 2017; Hunter & Yonzon, 1993). Thus, the Himalayas are an ideal place for testing a variety of biogeographical hypotheses, often related to species richness-elevation trends (Carpenter, 2005; Hunter & Yonzon, 1993; Li & Feng, 2015; Myers, 2003). In addition, mountain environments also provide perfect ecosystems to study the various responses of species to environmental changes by studying their shift over time with global warming, species vulnerability, their adaptive resilience (ultimately leading to speciation), and their phenological adjustment to climate clues (Catalan et al., 2017; Rödder et al., 2021; Wilson et al., 2005). Thus, the Himalayas hold great allure for ecological studies to achieve key insights into the association between ecological drivers and species diversity at multiple spatial scales (Bhattacharjee et al., 2017; Colares et al., 2021; Kattel, 2022; Rahbek, 2005; Shrestha et al., 2020).

Insects represent more than half of the Earth's biodiversity (Stork, 2018; Tihelka et al., 2021). They are essential components of nature and play a significant role in ecosystem functioning and ecological equilibrium (Hodkinson, 2005; Hodkinson & Jackson, 2005; Rosenberg et al., 1986; Scudder, 2017). Due to their high sensitivity and rapid response ability to environmental changes, they are considered good bioindicators (Chowdhury et al., 2023; Colares et al., 2021; Hodkinson & Jackson, 2005; Rosenberg et al., 1986). Therefore, many scientists have frequently used them to investigate the impact of environmental changes (Diamond et al., 2011), and thereby this knowledge can be applied to biodiversity management and the development of conservation action plans and policies (Akçakaya et al., 2006).

In biogeography, species generally exhibit two main distribution patterns along elevational gradients—apparent decline with increasing elevation and unimodal patterns (mid-elevation peaks) in species richness (Beck & Chey, 2008; Lomolino, 2001; McCain, 2009; Nathan et al., 2003; Rahbek, 2005). These two patterns are found to vary among species groups (Hu et al., 2017; McCain & Grytnes, 2010; Rahbek, 1995). But several studies postulated that the majority of taxonomic groups often supported unimodal trends along elevational gradients (Brehm et al., 2007; Colwell & Lees, 2000; Grytnes & Vetaas, 2002; Guo et al., 2013; Nathan et al., 2003; Rahbek, 2005; Rana et al., 2019). For instance, insect communities (Beck & Chey, 2008; Betz et al., 2020; Brehm et al., 2007; Choi, 2016; Kumar et al., 2009; Longino et al., 2019; Longino & Branstetter, 2019; Maicher et al., 2020; Munyai & Foord, 2015; Sanders, 2002; Toko et al., 2023; Yu et al., 2013), small mammals (volant and non-volant), birds and amphibians (Acharya et al., 2011; Cernohorska et al., 2020; Chettri & Acharya, 2020; Fu et al., 2006, 2007; Guo et al., 2013; Hu et al., 2017; McCain, 2003, 2005; Stevens et al., 2019; Wu et al., 2013a, 2013), and vegetation diversity (Bhattarai et al., 2004; Grytnes & Vetaas, 2002; Guo et al., 2013; Li & Feng, 2015; Oommen & Shanker, 2005; Sharma et al., 2019; Subedi et al., 2020; Zhou et al., 2019) widely displayed unimodal patterns in species richness along elevational gradients. Whereas, a few studies also revealed the monotonic decline of species along elevations in birds (Basnet et al., 2016; Blake & Loiselle, 2000; Ghimire et al., 2021; Hunter & Yonzon, 1993; Stotz, 1996), reptiles (Chettri et al., 2010), amphibians (Khatiwada et al., 2019), large geometrid moths (Axmacher et al., 2004), and small-ranged and non-endemic mammals (Chen et al., 2020).

It is widely accepted that the distribution and classification of biodiversity is mainly determined by complex biotic and abiotic factors integrated into elevational gradients (de Villemereuil et al., 2018; Grytnes & McCain, 2007; Han et al., 2021; Hodkinson & Jackson, 2005; Zhao et al., 2023). The species energy theory predicts that the trend for species richness' decline with elevation is due to decreased energy availability at the mountaintops (Beck & Chey, 2008; Lomolino, 2001), while productivity (Currie, 1991; Szewczyk & McCain, 2019; Vetaas et al., 2019), maximum humidity (Rahbek, 1995), water-energy dynamics (Diniz-Filho et al., 2010; Vetaas et al., 2019), and mid-domain effect (geometric constraints) (Colwell et al., 2004, 2016; Colwell & Lees, 2000; Letten et al., 2013; McCain, 2004; Sanders & Rahbek, 2012) have to be expected major factors for maximum species richness at mid-elevation. Among these factors, a mid-domain effect, despite facing criticism of its role in nature (Beck & Chey, 2008; Colwell et al., 2004), has been extensively studied and a new null model was proposed (Colwell & Lees, 2000). This model predicted that landmass boundaries limit species' ranges and tend to overlap at the middle of the gradient, leading to a peak in richness at the central point of the elevational gradients (Colwell & Lees, 2000; McCain, 2003, 2004; Zapata et al., 2003). Mid-domain effect cannot be recognized as an exclusive reason for the elevational distribution pattern of species, but the model has been used exponentially in explaining the spatial pattern combining with other ecological variables in all geographic levels (i.e., realms, latitudes or regions, elevations) (Colwell et al., 2004; Jetz & Rahbek, 2002; McCain, 2004). The spatial patterns of species are also found to be governed by various other ecological drivers such as climate variability, historical and evolutionary events, species-area effect, habitat heterogeneity, vegetation complexity, and ecotonal effect (Chettri & Acharya, 2020; Chown et al., 2013; Fu et al., 2006; Jetz & Rahbek, 2002; Lomolino, 2000; McCain, 2007; Pintor et al., 2016; Rosenzweig, 1992; Sharma et al., 2019; Szewczyk & McCain, 2019), and thus, these variables often apply to explain the impact of ecological amplitudes on species richness across geographic extent and spatial grain (García-Robledo et al., 2016; Hunter & Yonzon, 1993; Macedo et al., 2018).

Butterflies are widespread throughout the geographical space, that is, from tropical to high alpine meadow grasslands (Dewan et al., 2022). The variation in community composition along the spatial gradients may arise due to the differentiation of biogeography and niches within the species pool (Habel et al., 2023; Hodkinson, 2005; Popović et al., 2021). Therefore, butterflies play vital roles in multiple ecological services such as plant pollination systems, food chain, and indicators of climate change and healthier environments throughout the different geographical zones (Aguirre-Gutiérrez et al., 2016, 2017; Bonebrake et al., 2016; Chowdhury et al., 2023; Comay et al., 2021; Katumo et al., 2022; Oostermeijer & Van Swaay, 1998; Parikh et al., 2021; Pe'er & Settele, 2008). Hence, detailed understanding about the ecological services of butterflies is of primary concern for both long-term ecological monitoring programs and conservationist purposes.

Despite several studies to test the butterflies' response to ecological factors and their diversity changes along elevational gradients in other different parts of the world (Acharya & Vijayan, 2015; Comay et al., 2021; Despland, 2014; Despland et al., 2012; Dewan et al., 2021, 2022; Gallou et al., 2017; Habel et al., 2022, 2023; Leingärtner et al., 2014; Mtui et al., 2022; Pires et al., 2020; Sanchez-Rodriguez & Baz, 1995), such studies focusing on butterfly biodiversity have been poorly conducted in the trans-Himalayas of Nepal, except a few studies based on the short period data available within narrow elevational ranges (Pandey et al., 2017; Shrestha et al., 2020). Moreover, the response of montane butterflies to the ecological variables like vegetation productivity, surface temperature, moisture stress and landscape heterogeneity, which are known to have a great impact on butterfly distribution along elevation gradient in the mountain environment (Álvarez et al., 2024; Dewan et al., 2021, 2022; Seto et al., 2004), has not been clearly understood from the trans-Himalayas of Nepal. Therefore, in this study, we examined the response of overall butterfly species richness and their family-wise richness to these variables and richness–elevation relationship across wide elevational ranges (1600–5200 m above sea level [asl]). We addressed the following questions: (1) What are the patterns of overall butterfly species richness (hereafter simply called "richness") and family-wise richness (hereafter “subgroups”) of butterflies along the widest elevational gradients (1600–5200 m asl) in the trans-Himalayan region, Nepal? (2) How the remotely sensed environmental variables affect the richness and subgroups of butterflies along elevation gradients? We assume that elevational trends are not similar for richness and the subgroups. Finally, we also attempt to understand the role of environmental variables (which differ across elevational gradients) in demonstrating the biogeographical pattern of butterfly richness and their subgroups.

METHODS

Study area

This study was conducted in Manang district (28°27′–28°54′ N latitude and 83°84′–84°34′ E longitude; area: 2246 km^2), a part of the trans-Himalayas located in north-central Nepal, and falls under the Annapurna Conservation Area (ACA). The district stands within an elevational range of 1600–8156 m asl. Geographically, the district is surrounded by the crest of the Great Himalayan Mountain ranges, that is, Manaslu Mountain (east), Damodar and Muktinath Mountains (west), Annapurna and Lamjung Mountains (south), and the Peri, Himlung, and Cheo Mountains (north) (Bhattarai et al., 2006). The district experiences a vast variation in ecological gradients that comprises subtropical (0.3%), temperate (3.7%), subalpine (14.6%), alpine (13.9%), nival (25.4%), and trans-Himalayan (41.1%) ecosystems. Owing to such heterogenous gradients, the district exhibits diverse flora ranging from subtropical to alpine. The subtropical and temperate plant diversity such as *Pinus wallichiana*, *Rhododendron arboreum*, *Arundinaria intermedia*, *Juglaens regia*, *Picrorhiza species*, *Rheum emodi*, *Daphne bholua*, *Betula utilis*, *Glycyrrhiza glabra*, *Tsuga dumosa*, *Berberis* species, *Anaphalis* species, *Artemisia* species, and *Anemone* species are widely found from lower Manang (1700 m asl) to the subalpine regions of the mid Manang (3500 m asl) (Ghimire et al., 2021; Khanal, 1982; Shrestha et al., 2020). Pines are the dominating flora in the mid-elevation (2800–3400 m asl) while subalpine and alpine vegetations like *P. wallichiana*, *Rhododendron campanutum*, *Juniperus recurva*, *Iris kamaonensis*, *Astragalus* species, *Nardostachys jatamansi*, and *Orchis latifolia* are distributed with higher density between 3600 and 4200 m elevation ranges (Ghimire et al., 2021; Khanal, 1982). Along the entire mountain arc, the treeline is formed within 4000–4200 m asl (Schickhoff et al., 2015) and above the treeline ecotone, alpine scrubs and meadows dominate the region. The foothill of the district experiences a humid climate, while the high-altitude areas are cold almost throughout the year. Marsyangdi, a major mountain river of the district, flows eastward through the central coastal depth of Manang forming a U-shaped valley to the district (Pohle, 1990). The rainy season generally ranges from March to end of October while snow is common during winter (December–February) above 2400 m asl. According to the Meteorological Department of Humde, 2021, the average premonsoon and monsoon precipitation received over the six years was measured at 135 and 185 mm, respectively. The district experienced the hottest month in June and the coldest in January with average maximum and minimum temperatures reaching 15 and −11°C in these months, respectively.

Data collection

Environmental variables

We downloaded a gap-filled modified SRTM-derived 30-m resolution digital elevation model (NASA JPL 2020) available on Google Earth Engine to classify 200-m elevational bands for the study area. Along with the elevation data, other important variables that might impact the richness of butterfly species like productivity, temperature, and moisture (Álvarez et al., 2024; Dewan et al., 2021) were estimated using remotely sensed data and topography. Spatial heterogeneity was calculated from available open-source data. Specifically, we calculated the mean normalized difference vegetation index (hereafter NDVI) from 2015 to 2022 from cloud and cloud shadow-masked LANDSAT 8 imagery using Google Earth Engine to estimate the average productivity of the landscape during the survey time (2018–2022). Similarly, we used the thermal band from the same remotely sensed data to estimate the surface temperature of the landscape during the time. Furthermore, the same Landsat data were used to estimate the moisture stress index; a remote sensing index that estimates the lack of moisture in soil or plants (Hunt & Rock, 1989) and is an effective predictor of soil moisture condition (Welikhe et al., 2017; Wickham, 2016). Finally, we downloaded global land cover data from Sentinel 2 imagery available at the resolution of 10 m for the year 2021 (Karra et al., 2021), resampled it to the resolution of other variables (30 × 30 m), and calculated the Shannon–Weiner index of the land cover to estimate the richness of land cover type within the moving window of 3 × 3 pixel size (hereafter heterogeneity; Koirala et al., 2022) using “landscape metrics” package (Hesselbarth et al., 2019) in R (R Core Team, 2021). We also calculated the percentage area of rangeland; land cover type classified as grasslands and shrublands, in a moving window of 3 × 3 pixel size (hereafter proportion of rangeland) and used it as an explanatory variable. Finally, the available Digital Elevation Model (DEM was used to calculate the slope which was used as a topographical variable for the study. The average values of the environmental variables in each elevational band were used to model the relationship between species richness and the selected environmental variables. A multicollinearity test between the selected variables was performed to remove redundant information before running the model.

Species richness

The sampling of butterflies was carried out over five periods in three different years—May and October 2018, June and August 2019, and April/May 2022—which were considered the appropriate timing for the butterflies' survey in the Himalayas due to there being absence of snow. The data were collected within the elevations ranging from 1600 to 5200 m asl. Transect count or "Pollard Walk" is the extensively used method for butterfly surveys (Isaac et al., 2011; Kitahara, 2004; Pellet et al., 2012; Pollard, 1977); however, we used a fixed-point count method along the permanent transects in every altitudinal gradient to collect data (Acharya & Vijayan, 2015). This method is highly recommended and considered the best butterfly sampling technique, specifically in the difficult Himalayan topography (Acharya & Vijayan, 2015; Bhardwaj et al., 2012; Dewan et al., 2021; Henry et al., 2015; Kral et al., 2018). Due to geographically difficult terrain (rugged and sloppy) and lack of more open space in the sampling sites, we did not replicate transects in each elevation gradient. Thus, based on the proportion of areas of the sampling gradients (Rosin et al., 2012), a single transect of 500–700 m length was permanently established throughout the gradients at every 200 m elevational band, hence obtaining 19 sampling bands in total (Figure 1). This interval was designated to permit fine-scale assessment of butterfly richness along every

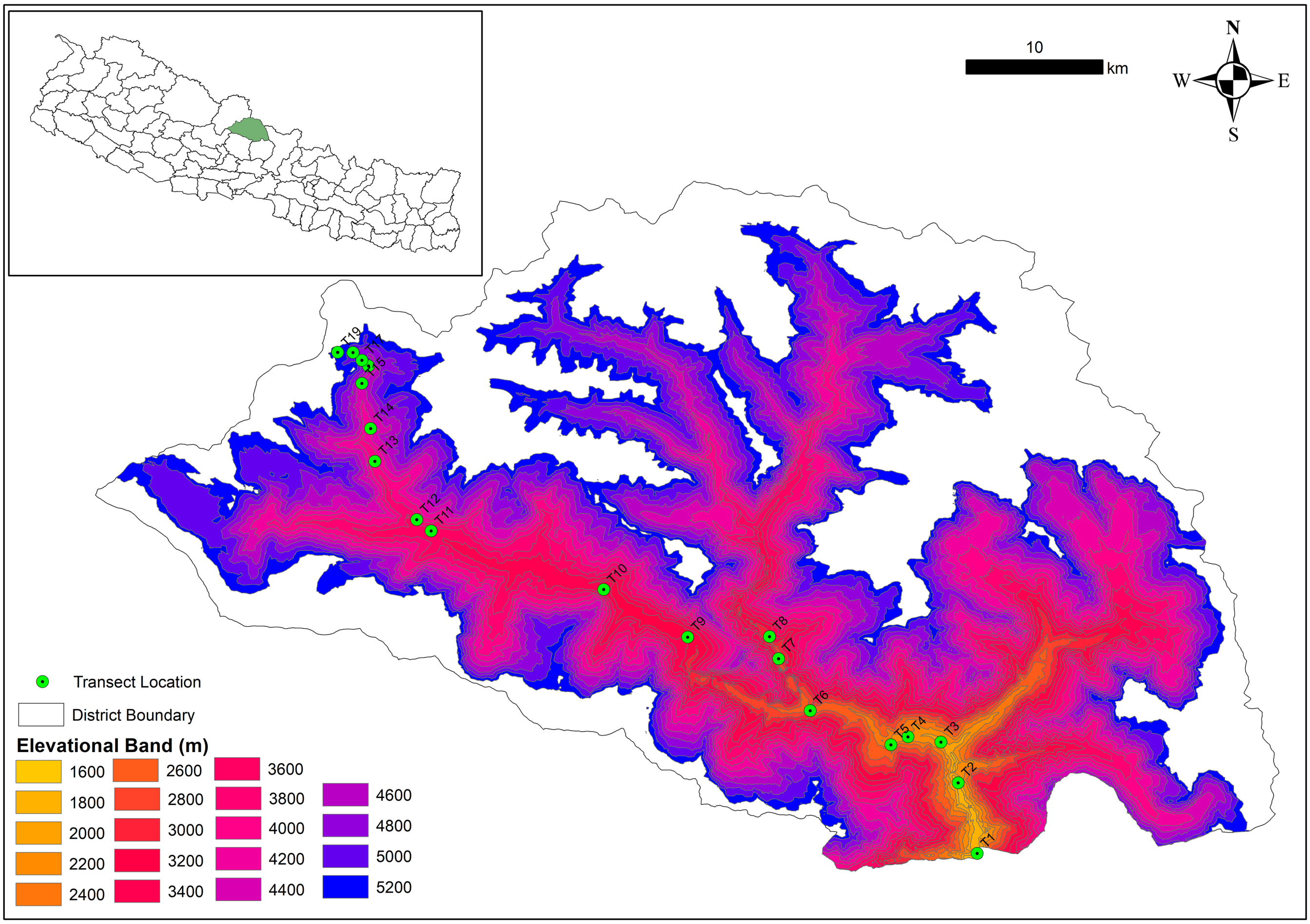

FIGURE 1 Map of Manang district showing the sampling transects along the elevation gradients.

sampling gradient and to restrict the double count of the same species during regular sampling periods. The transects were run through the existing zigzag patrolling foottrails, trekking routes, and roads, and maintained within walking distance. GPS (Garmin etrex 30×) (with an accuracy of ±3 m) was used regularly to fix the size of the transects, inter-plot distances, and elevational position. Within each transect, 6–9 permanent plots (depending upon the length of the transect) each with 5 m radius from the center of the plot were set for butterfly sampling. The interval between the two consecutive plots was marked 70–80 m in order to avoid recounting of same butterfly individuals during sampling (Dewan et al., 2021). Altogether, 152 sampling points were established throughout the gradients. Survey of butterflies was often conducted between 9:00 and 14:00 h (Dewan et al., 2021; Shrestha et al., 2020; Subedi et al., 2021) under favorable weather conditions (having 20% cloud cover and light wind days). However, due to sudden changes in weather conditions, sampling was not done in August 2019 and May 2022 above 4400 m. All points were replicated 1–3 times each, thus, we conducted 1724 point counts in total throughout the study periods.

Most of the butterflies were studied under direct observation (15 min per plot visit) in the plots. Additionally, the species observed at ±50 m of the sampling elevation point was assumed to be present within this range (Dewan et al., 2022; Stevens, 1992). A capture–release method was deployed for the correct identification of cryptic butterflies (Khanal et al., 2012; Pellet, 2008) and any unidentifiable butterflies were photographed for further confirmation through expert consultations (Acharya & Vijayan, 2015; Dewan et al., 2021; Pandey et al., 2017). The morphology of wings was carefully studied for correct taxonomic determination of the butterflies and cross-validated with published literature (Khanal, 1982, 1984; Smith, 2011; Van Der Poel & Smetacek, 2022). To estimate the butterfly species richness (*n*) at each elevation band, we employed an interpolated richness based on the species recorded at the lowest and the highest elevation ranges (Bhattarai et al., 2004; Grytnes & Romdal, 2008; Grytnes & Vetaas, 2002; Hu et al., 2017; Hunter & Yonzon, 1993). It is well known that species richness may vary along elevational gradients, and in various aspects in mountain environments, but the interpolated species richness provides one absolute value of richness estimation for each elevational band (Ferrer-Casten & Vetaas, 2003; Hu et al., 2017; Panthi et al., 2007). Abundance of butterflies was not collected in this study due to the complexities of counting within the intricate biophysical gradients, particularly between 2000 and 2600 m asl, and above 4200 m asl.

Data analysis

Clustering of butterfly communities along elevational zones

To determine the elevational ranges covered by butterfly assemblages across elevational gradients in the study area, we used K-means clustering in "factoextra" package (Kassambara & Mundt, 2020) on a data matrix that consisted of elevation and species presence/absence data in R program.

We excluded the family Riodinidae from the analysis since only two species were recorded throughout the study period. However, they were not excluded in the final results of diversity and elevational range cover.

Response to elevational gradients and selected environmental variables

We determined the relationship between the observed data of richness and subgroups of butterflies across the altitudinal gradient in the trans-Himalayan region using multivariable modeling techniques. Firstly, we modeled the response of richness and each of subgroup within the elevational gradients using a generalized linear model with the Gaussian family and identity link functions. We also tested quadratic and cubic terms to check for other dominant trends of species richness along elevation gradients. All models were then compared using Akaike information criterion (Burnham & Anderson, 1998), and the most parsimonious model ($\Delta \text{AIC}_c = 0$) was selected for the inference. We chose to use the most parsimonious model rather than a multimodel inference because the most parsimonious model was the only model that met the requirement of $\Delta \text{AIC}_c < 2$ criteria for multiple models.

To determine the response of the selected environmental variables on the species richness of butterflies, we used the same model family and link functions as used to assess the elevational gradient but performed a dredging function in the "MuMin" package in R (Bartoń, 2022) where all possible linear combinations of the environmental variables were run. The final model was selected by using the criteria of $\Delta \text{AIC}_c < 2$ for multimodel inference. All data visualization was done using the ggplot2 package (Wickham, 2016) in R. The environmental factors and elevation were used as explanatory variables. The relationships between elevation and environmental factors were quantified using Pearson's correlation coefficient and visually by line plots.

RESULTS

Diversity and distribution of butterflies along elevation gradients

A total of 94 butterfly species, belonging to 60 genera, representing 20 subfamilies and six families were recorded throughout the study (Appendix S1: Table S1). Nymphalidae showed the highest species diversity ($n = 41$) throughout the study periods accounting for 43.62%, followed by Lycaenidae ($n = 20$; 21.28%), Pieridae ($n = 13$; 13.83%), Papilionidae ($n = 10$; 10.64%), Hesperiidae ($n = 8$; 8.51%), and Riodinidae ($n = 2$; 2.13%) (Figure 2).

The K means clustering analysis showed a distinct distribution pattern of butterfly communities along the elevational zones. This clustering categorization showed that 39 butterfly species (41.5%) (Nymphalidae: 19 spp.; Pieridae: 5 spp.; Hesperiidae: 5 spp.; Papilionidae: 5 spp.; Lycaenidae: 4 spp.; and Riodinidae: 1 spp.) occurred below 2400 m asl. Furthermore, 19 butterflies were found restricted in a single elevation band whereas six species, namely *Aglais caschmirensis*, *Colias fieldii*, *Pieris brassicae*, *Lampides boeticus*, *Papilio machaon*, and *Vanessa cardui* occurred within a broad elevational range (Figure 3). Among them, *A. caschmirensis* was the only butterfly registered at the broadest elevation range (i.e., 1600–5000 m asl) (Figure 3).

Elevational patterns of butterfly species richness

All three models (linear, quadratic, and cubic) were supported by the richness and subgroups of butterflies, hence detecting a variety of elevational patterns of butterflies (Table 1; Figure 4). Lycaenidae butterfly was best explained by a linear model, Nymphalidae and Pieridae fitted best with quadratic, and cubic function was found the best-suited model to the richness, and subgroups Papilionidae and Hesperiidae (Table 1, Figure 4). Among them, Lycaenidae showed a strong monotonic decline in

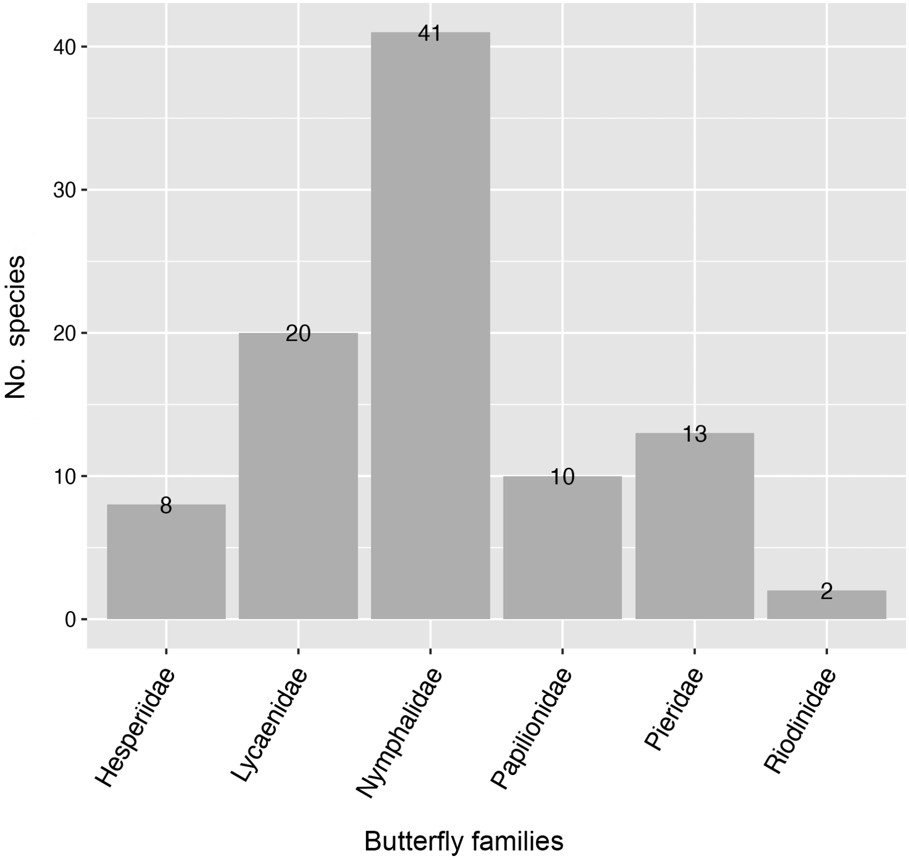

FIGURE 2 Numbers of butterfly species representing six butterfly families in the study sites.

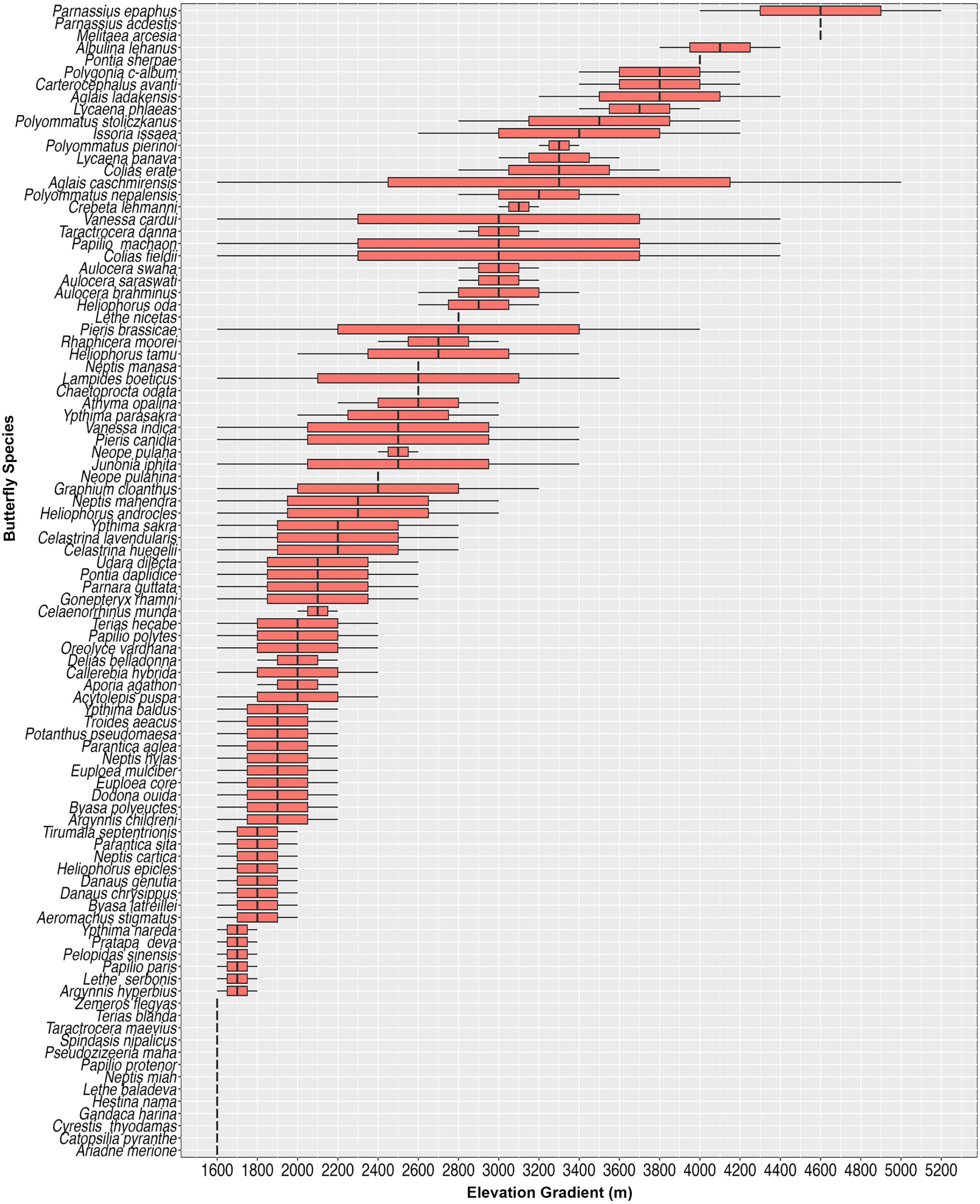

FIGURE 3 Elevation ranges covered by each butterfly species in Manang, trans-Himalayas, Nepal. Each band represents the interquartile range (IQR), which covers the middle 50% of the species data points along an elevation range. The midline of each boxplot indicates median elevation of the species distribution. Upper and lower whiskers on each band show maximum and minimum elevation ranges.

TABLE 1 Summary of results of generalized linear models of richness and subgroups of butterflies considering response variables as a function of elevation.

Butterfly assemblages	Models	ΔAIC_c	Intercept (SE)	Coeff. linear	Coeff. quadratic	Coeff. cubic
Richness	**Cubic**	0	141.1 (5.190e−10)	−0.074	0.01523	−1.21e−09***
	Quadratic	2.14	1.023e+02 (5.585e−07)	−3.426e−02	2.855e−06	
	Linear	17.28	72.76 (0.00086)	−0.015		
Nymphalidae	Cubic	1.31	6.004e+01 (3.478e−10)	−7.373e−02	1.523e−05	−1.213e−09
	Quadratic	0	4.405e+01 (3.418e−07)	−3.426e−02	2.855e−06***	
	Linear	8.51	72.76 (0.000441)	−0.014851		
Lycaenidae	Cubic	2.27	4.455e+00 (1.810e−10)	7.939e−03	−3.280e−06	3.010e−10
	Quadratic	1.73	1.408e+01 (1.815e−07)	−1.852e−03	−2.101e−07	
	Linear	0	16.26 (0.00018)	−0.0033***		
Pieridae	Cubic	3.61	1.720e+01 (1.431e−10)	−6.207e−03	7.982e−07	−4.935e−11
	Quadratic	0	1.562e+01 (1.324e−07)	−4.602e−03	2.949e−07*	
	Linear	1.88	12.5649123 (0.00014)	−0.002597		
Papilionidae	**Cubic**	0	3.671e+01 (1.117e−10)	−2.714e−02	6.897e−06	−5.776e−10***
	Quadratic	15.69	1.824e+01 (1.716e−07)	−8.351e−03	1.006e−06	
	Linear	71.54	7.8140351 (0.00029)	−0.0015088		
Hesperiidae	**Cubic**	0	2.274e+01 (1.067e−10)	−1.711e−02	4.450e−06	−3.875e−10**
	Quadratic	8.23	1.034e+01 (1.347e−07)	−4.506e−03	4.976e−07	
	Linear	52.27	5.186 (0.000174)	−0.0011228		

Note: Linear, quadratic, and cubic models are tested to determine best-suited models and ranked by ΔAIC_c values. Best suited models appear in boldface. Significant values of model coefficients (Coeff.): $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Abbreviation: AIC_c, corrected Akaike information criterion.

species diversity, whereas richness, Nymphalidae and Pieridae exhibited a gentle decline in species diversity with increasing elevation (Figure 4). Papilionidae and Hesperiidae showed a significant monotonic decline up to the elevational band at 3200 m asl and remained roughly constant till subsequently exhibiting a decline trend after 4400 m asl toward the end of the elevational gradients (Figure 4). This study showed all suitable models predicted declining patterns with increasing elevations and none of the models predicted a peak at intermediate elevation (Figure 4).

In terms of relationships between environmental variables and elevation, only NDVI showed a strongly negative correlation ($r = -0.94$) (Figure 5). The other variables did not show any significant correlation with elevation (Figure 5).

Responses of butterfly species richness to environmental variables

Our models suggested that NDVI had a strong positive correlation with richness ($p < 0.001$) and subgroups of butterflies (Nymphalidae, Lycaenidae, and Pieridae; $p < 0.001$, Papilionidae; $p < 0.05$, and Hesperiidae; $p < 0.01$) (Table 2). Additionally, Papilionidae and Hesperiidae showed a significant negative relationship to moisture stress and were positively associated with surface temperature and landscape heterogeneity (Table 2). Surprisingly, our model did not detect any significant effects of these variables on richness and other subgroups of butterflies (Table 2).

DISCUSSION

This is the first comprehensive study to determine richness–elevation relationships of butterfly diversity within wider elevational ranges in the Himalayas Nepal. Moreover, we also determined the impact of ecological drivers on butterfly diversifications across the elevational gradients. This study expanded upon a previous study that only covered the mid-elevation of the study sites (Shrestha et al., 2020) and assessed the diversity of butterflies of the trans-Himalayan region after nearly four decades covering such as a wider elevational range. The present study covered 13.6% and more than 25% of the total butterflies of Nepal and ACA, respectively. The

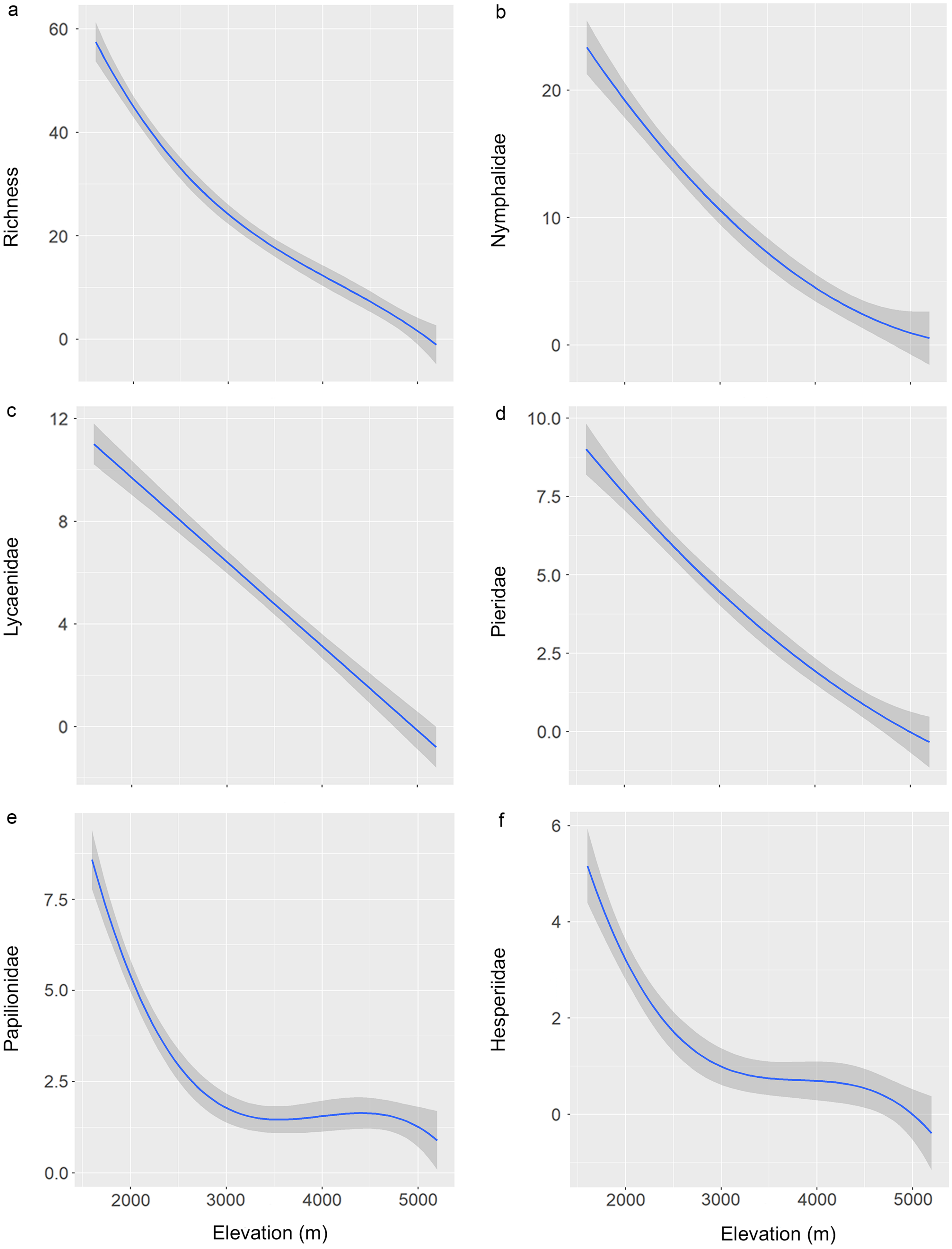

FIGURE 4 Relationships between elevation and (a) richness and subgroups of butterflies, (b) Nymphalidae, (c) Lycaenidae, (d) Pieridae, (e) Papilionidae and (f) Hesperiidae along the elevation gradients. Solid lines represent the fitted model (R ggplot). Shaded areas around curve represent 95% confidence interval.

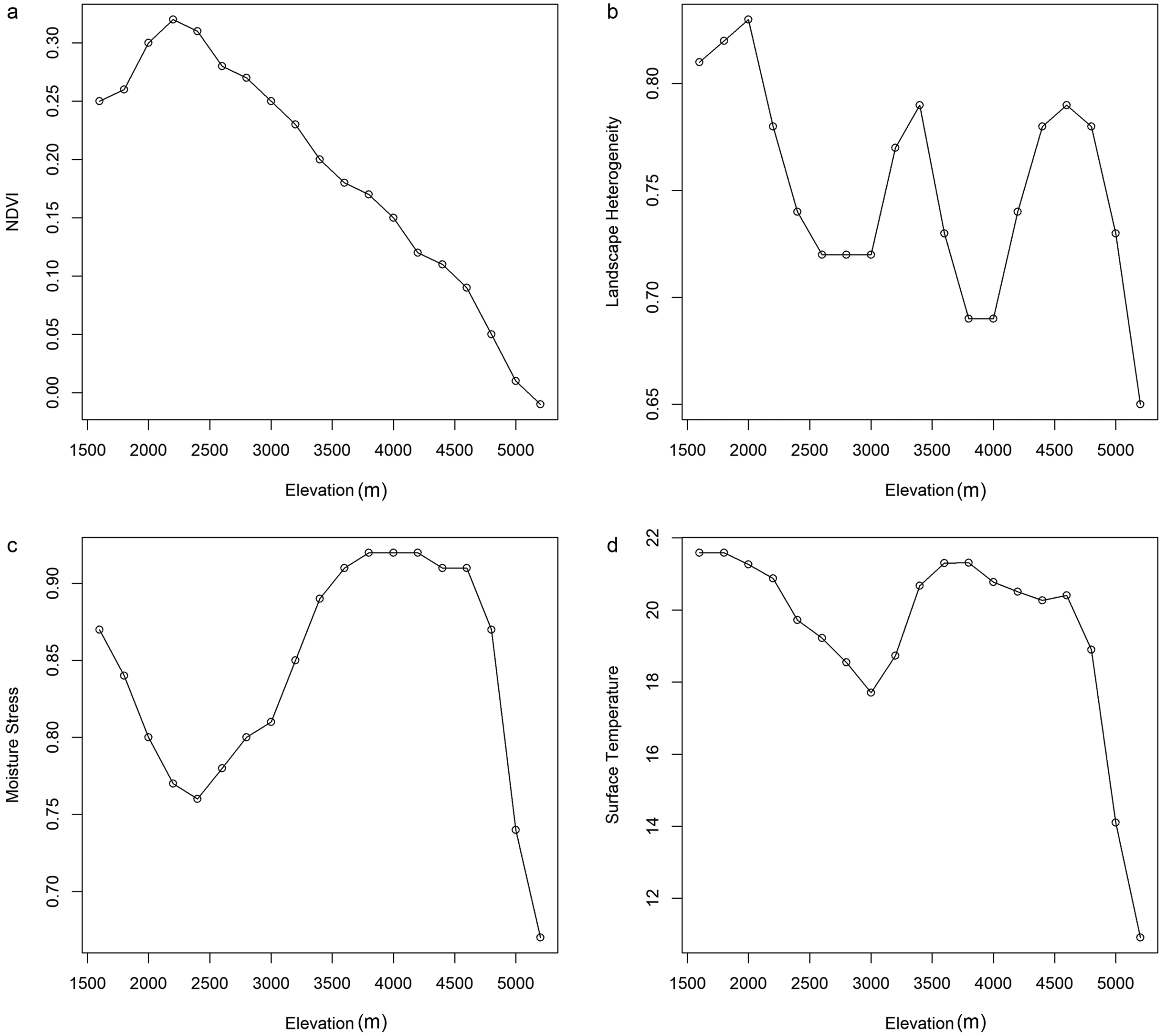

FIGURE 5 Relationships between elevation and the measured environmental variables to determine the species richness of butterflies in the trans-Himalayas, Nepal. NDVI, normalized difference vegetation index, which estimates the average productivity of the landscape.

study revealed a dominance of Nymphalidae butterflies within the study sites, which is similar to what we expected as they are the largest family covering 34.5% of the total butterflies of Nepal. This result is consistent with previous records from Manang (Khanal, 1982, 1984; Shrestha et al., 2020), other regions of Nepal (Khanal et al., 2012; Pandey et al., 2017; Subedi et al., 2021), and other mountainous regions elsewhere (Dewan et al., 2021; Gallou et al., 2017; Mtui et al., 2022). The strong association of Nymphalid butterflies with host range variability and greater vegetation diversity than other subgroups of butterflies along the multiple spatial scales (local and regional) (Nylin et al., 2014; Shrestha et al., 2020) and being a more diverse group of butterflies (Wiemers et al., 2018) might be potential reasons for the dominance of Nymphalids in the study sites.

We found most butterflies occupied narrow elevation bands, particularly below 2400 m asl (41.5%), and 20% of the species occurred only at a single elevational band. Our results are consistent with the findings of previous studies on butterflies in the Himalayas of Sikkim, India (Dewan et al., 2021, 2022; Sharma et al., 2020). The narrow elevation range of butterflies can be attributed to their dependency on specific host plants, and associated with habitat variations caused by steep elevational gradient (Atauri & De Lucio, 2001; Levanoni et al., 2011; Pellissier et al., 2012), which may be linked with the life history of butterflies that

TABLE 2 Summary of results of generalized linear models of the relationships between richness and subgroups of butterflies, and environmental variables.

Models		Estimate	SE	*Z*-value	*p*-value
Richness	Intercept	−48.3	40.79	1.136	0.256
	NDVI	129.5	23.24	5.197	**2.00e−07*****
	Sh_in	98.97	46.96	1.95	0.0512
	MSI	−37.83	29.05	1.198	0.2311
Nymphalidae	Intercept	−20.1698	17.9362	1.076	0.2817
	NDVI	56.5045	10.8364	4.862	**1.16e−06*****
	Sh_in	44.3163	22.6085	1.818	0.0691
	ST	−0.6315	0.4734	1.227	0.22
	MSI	−16.9187	13.3453	1.166	0.2437
Papilionidae	Intercept	−10.2334	10.5796	0.94	0.34721
	NDVI	8.1323	3.8208	1.968	**0.04909***
	Sh_in	23.0591	9.0644	2.372	**0.01768***
	ST	0.6083	0.2534	2.257	**0.02401***
	MSI	−20.969	7.4747	2.598	**0.00938****
Lycaenidae	Intercept	−1.9879	5.1769	0.366	0.714
	NDVI	34.5811	4.2786	7.539	**2.00e−16*****
	Sh_in	10.9724	8.9957	1.136	0.256
	ST	−0.2328	0.2551	0.853	0.394
	MSI	−3.5301	8.1546	0.406	0.685
Pieridae	Intercept	−3.0773	7.1563	0.418	0.675864
	NDVI	22.8299	6.012	3.649	**0.000263*****
	Sh_in	12.6826	7.4154	1.583	0.113508
	ST	0.7524	0.3634	1.904	0.056898
	MSI	−16.143	12.643	1.225	0.220558
Hesperiidae	Intercept	−3.4256	6.773	0.496	0.61996
	NDVI	7.8953	2.8237	2.61	**0.00906****
	Sh_in	12.4955	5.5467	2.083	**0.03727***
	ST	0.5825	0.1353	3.982	**6.84e−05*****
	MSI	−16.01	5.0401	2.937	**0.00332****

Note: Significant values of model coefficients appear in boldface.
Abbreviations: MSI, moisture stress index; NDVI, normalized difference vegetation index; Sh_in, Shannon index; ST, surface temperature.

interplays with range size determinants (Brehm et al., 2007; Hodkinson, 2005; Pires et al., 2020) or the threshold zone of adaptation (ecological niche). In addition, the distinct ecotonal zone, composed of rich shrubby vegetation diversity in temperate ecosystems (<2400 m) (Panthi et al., 2007), might have offered high-quality food resources to butterflies rather than coniferous to alpine meadow ecosystems (>2600 m asl) and hence supported a greater number of butterflies at low elevation ranges (Acharya & Vijayan, 2015; Despland et al., 2012; Dewan et al., 2022; Gallou et al., 2017). Our study found no conclusive evidence for those species being restricted to the single elevational band. Therefore, future studies related to the physiology, phenology, and behavioral response of these butterflies to microclimate (topography, temperature, soil, and vegetations) variations and changes in resource availability along elevation gradients are necessary to reach a final conclusion. We also detected butterfly species like *A. caschmirensis*, *V. cardui*, *Pieris brassicae*, *P. canidia*, *Colias fieldii*, *Papilio machaon*, and *L. boeticus* covering the broadest elevation ranges. This could be explained by the butterfly species being linked to life history traits such as habitat generalists, extensive dispersal ability, and strong tolerance of greater climatic and topographic variability (Cómbita et al., 2022).

Our study that examined the patterns of observed richness and subgroups of butterfly communities along the broadest elevation gradients in the trans-Himalayan region of Nepal showed decreasing patterns of butterfly diversity with increasing elevations. But our model did not show a unimodal pattern of mid-domain effect, a commonly suggested distribution pattern of biodiversity along elevational gradients (McCain & Grytnes, 2010; Rahbek, 1995, 2005) nor any evidence of a continuous curve against elevational gradients. Hence, our study indicated that butterflies are not constrained by geographic hard boundaries. Similar results have also been obtained in other studies on various taxa including Lepidoptera (Acharya & Vijayan, 2015; Beck & Chey, 2008; Bhardwaj et al., 2012; Chettri, 2015; Dewan et al., 2021; Kumar et al., 2009; Leingärtner et al., 2014; Sanchez-Rodriguez & Baz, 1995), ant diversity in the southern Costa Rica (Longino & Branstetter, 2019), vertebrates like reptiles (Chettri et al., 2010), and birds (Basnet et al., 2016; Ghimire et al., 2021; Terborgh, 1977, 1985). Therefore, a decline in biodiversity richness with increasing elevation is now considered a general trend (Brown & Lomolino, 1998; Dewan et al., 2021; Whittaker & Niering, 1965). However, an increase in species richness (Kaltsas et al., 2018; Shrestha et al., 2020) and a bimodal pattern (Popović et al., 2021) have also been accepted. Our results support the hypothesis that predicts when all elevation gradients were considered, the findings were often hump-shaped but, as the scale decreases, such a relationship would likely gradually change into a diminishing pattern (Nogue's-Bravo et al., 2008). The results of our study indicate that the high-altitude butterflies were mostly habitat specialists (Ehl et al., 2019; Habel et al., 2023; Mtui et al., 2022), and the geographical contractions restrict the dispersal ability and their behavioral plasticity in multiple spatial scales (Habel et al., 2022; Saastamoinen et al., 2010; Van den Heuvel et al., 2013). In addition, the decline of the spatial scale of butterfly diversity in high altitudes might be associated with different environmental variables such as reduced temperature and rainfall (Acharya & Vijayan, 2015; Ehl et al., 2019; Pollard, 1988; Rahbek, 1995), a decrease in vegetation richness (Hawkins & Porter, 2003; Pe'er & Settele, 2008; Pires et al., 2020; Rahbek, 2005), steep slopes, and harsher weather like snow cover in the montane environment (Chettri et al., 2010; McCain, 2007). Thus, this study to a certain extent confirms that biogeographical affinity may interact with elevation to produce different trends in species diversity through the modulating effect of ecological factors.

In addition to elevation patterns of subgroups of butterflies, only Lycaenidae exhibited a monotonical decline of species with increasing elevations. Similar to our results, a previous study also found a monotonic decline in Lycaenidae butterfly diversity with increasing elevation (Dewan et al., 2021). This kind of distribution pattern in Lycaenids is probably due to low vagility and dispersal ability (being small-sized) in topographically heterogenous landscapes, and precise environmental requirements like less stressful microclimate conditions (New, 1993) and monophagous habitat specialists (Edge & Mecenero, 2015).

We did not explicitly examine the impact of all potential environmental variables on the richness and subgroups of butterflies along elevational gradients. We examined the effect of four environmental variables that can generate insights into the impact of spatial distribution of butterfly diversity along elevation gradients. We predicted the mean values of these four variables using satellite-derived indices. It is suggested that the commonly used remotely sensed indices are the most efficient estimate to predict butterfly patterns in the spatial land cover ecology (Bailey et al., 2004; Kerr et al., 2001; Levanoni et al., 2011; Seto et al., 2004). We found NDVI was a significant predictor of richness and subgroups of butterflies. Our findings are consistent with previous studies on butterfly richness (Bailey et al., 2004; Seto et al., 2004), and other faunas, for instance birds (Ghimire et al., 2021; Pandey et al., 2017; Seto et al., 2004) and small mammals (Chen et al., 2020). The relatively strong correlation obtained here between NDVI and butterfly communities across the spatial gradients is not surprising, as this is simply due to the fact that NDVI decreases with elevation (Figure 5), resulting in less resources at higher elevation for butterfly communities (Bailey et al., 2004; Dewan et al., 2021; Seto et al., 2004). In general, lowland butterflies are often governed by water energy variables (Despland et al., 2012; Diniz-Filho et al., 2010), and their effect implies that species richness on elevation gradients is correlated with productivity (McCain, 2010). Similarly, in our study gradients, productivity and butterfly diversity is highest at the lower elevations. Thus, our study supports the productivity hypothesis which suggests that more biomass (i.e., productivity) supports greater species diversity in an area (Gillman et al., 2015; Grytnes & McCain, 2007; Šímová et al., 2013; Waide et al., 1999). In contrast to our result, mean NDVI was found to have a weak and not significant relation with butterfly diversity along elevation gradients in previous study (Levanoni et al., 2011). However, contradicting the previous perception of the relationship between butterfly diversity and NDVI by Levanoni et al. (2011), our study suggests

NDVI can be an efficient predictor that determines the species richness–elevation relationship and may serve as an exceptional test system for evaluating the importance of productivity on species distribution patterns.

We obtained marked differences among the subgroups in terms of association with the other estimated environmental parameters. Papilionidae and Hesperiidae butterfly diversity have shown significant responses to all four environmental factors (Table 2). Our findings can be attributed to the butterflies belonging to these families being very sensitive to environmental changes and to small variations in environmental variables having a significant influence on major changes in their assemblages in montane environments (Bauder et al., 2015; Yu et al., 2023). Therefore, it can be alleged that the butterflies from these subgroups are habitat specialists depending on multiple environmental variables (Bauder et al., 2015) and are less tolerant to extreme climatic vulnerability in the mountain environments. However, studies of functional ecology in the multiple spatial scales of the Himalayas would provide a better understanding of the relationship between species and environmental parameters.

CONCLUSION

This study indicated that butterfly communities were found to be not uniformly distributed along the elevational gradients in Manang, trans-Himalayan region, north-central Nepal. Additionally, in terms of altitudinal distribution suitability, most butterflies (i.e., 41.49%) exhibited low altitude zone ranges (below 2400 m asl) and narrow elevational ranges, where 19 species occurred at only a single altitudinal band. This suggests butterflies follow limited range sizes in high-altitude gradients, probably by a combination of dispersal ability, host-specificity, and threshold of environmental tolerance. However, more research is now required on the functional traits of butterflies, particularly habitat specialists and generalists, as well as their life history to understand further related to the major causes of their distribution along spatial gradients. The present study also revealed that the response of montane butterfly communities toward environmental variables varies among subgroups of butterflies; however, NDVI was the major environmental factor determining butterfly assemblage across elevational gradients. These quantitative results presented here will allow the prediction of the effect of climate change and distribution modeling in montane butterflies in the future. Moreover, our results will also help in assessing the dynamics and conservation status of butterflies over time in the Himalayan region of Nepal. Lastly, this study reveals the importance of remote sensing data at levels of resolution comparable to field data and confirms the dependence of relationships between environmental predictors and species richness on altitudinal scales.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Shrestha et al., 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.8388959.

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