Butterfly communities along the elevation gradient of Sikkim: Distribution pattern and phylogeny of select species

A Thesis Submitted

To

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Degree of Doctor of Philosophy

By

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This is to certify that the Ph. D thesis **entitled "Butterfly communities along the elevation gradient of Sikkim: Distribution pattern and phylogeny of select species"** submitted to Sikkim University in partial fulfillment for the requirements of the degree of Doctor of Philosophy in Zoology embodies the research work carried out by **Mr. Sailendra Dewan** at the Department of Zoology, School of Life Sciences, Sikkim University under our supervision. The results are original and have not been submitted anywhere else for any other degree or diploma.

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"Butterfly communities along the elevation gradient of Sikkim: Distribution pattern and phylogeny of select species"

Submitted by **Mr. Sailendra Dewan** under the supervision of **Dr. Bhoj Kumar Acharya**, Associate Professor & Head and Co-supervision of **Dr Sudeep Ghatani**, Assistant Professor, Department of Zoology School of Life Sciences, Sikkim University.

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I, Sailendra Dewan, declare that the present Ph. D thesis entitled "**Butterfly communities along the elevation gradient of Sikkim: Distribution pattern and phylogeny of select species**" submitted by me for the award of the degree of Doctor of Philosophy in Microbiology of Sikkim University under the supervision of Dr. Bhoj Kumar Acharya, Associate Professor, Department of Zoology, Sikkim University and co-supervision of Dr. Sudeep Ghatani, Assistant Professor, Department of Zoology, Sikkim University, is a original research work solely carried out by me in the Department of Zoology, Sikkim University, Gangtok.

The thesis contains no material that has been accepted for the diploma or degree of any University or Institution, except by the way of background information and duly acknowledged in the thesis, and in my belief no materials previously published or written by another person except where due acknowledged is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Sailendra Dewan

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CHAPTER 1

INTRODUCTION

1.1 Background

The living organisms are not randomly distributed across space and time and are reported to follow some logical pattern (Rahbek, 1995). Understanding the distribution pattern of organisms across large spatial gradients and unraveling the underlying processes has been one of the key topics of research in biogeography and conservation biology (Stevens, 1992; Sánchez-Rodríguez & Baz, 1995; Rahbek, 2005; Acharya et al., 2011a; Wu et al., 2013a; Li & Feng, 2015; Rana et al., 2019). Such information serves as a baseline for understanding the effect of climate change on biological assemblages (Hodkinson, 2005) and aids in identifying diversity hotspots that need to be prioritized for conservation (Hunter & Yonzon, 1993; Bhardwaj et al., 2012; Chettri, 2015; Chettri & Acharya, 2020). Much studies has been undertaken across region and taxa along spatial and environmental gradients but the patterns and process that shapes the diversity and distribution of life on earth is not yet properly understood (Rahbek, 2005; McCain & Grytnes, 2010; Sanders & Rahbek, 2012).

Studies along the large spatial gradient have been mostly conducted along the two frontiers; (i) the latitudinal and (ii) the elevational gradient. The majority of studies focusing on the latitudinal gradient have consistently found a decline in species number and density from the equator to poles (Pianka, 1966; Stevens, 1989; Gaston & Blackburn, 2003). Similar to latitudinal gradients, mountain experiences variation in spatial and ecological factors along the smaller scale such as elevation. The distribution of biodiversity in mountains also varies, with space and time (McCain & Grytnes, 2010; Hendershot et al., 2017). As compared to latitudes, mountains offer additional characteristics that make them perhaps more suitable for uncovering the underlying causes of spatial variation in diversity in many ways (Sanders & Rahbek, 2012). Firstly, there are many mountains ranges which may act as replicates of elevation diversity gradients; so it is possible to test for the generality of the underlying causes. Secondly, it is possible to carry out manipulative experiments along elevation gradients. Thirdly, as the spatial extent of the elevation gradient in a mountain is relatively smaller than the latitudinal gradient, it is much easier to undertake well designed field studies.

While elevation was previously thought to proxy the latitudinal gradient in diversity trends (Stevens, 1992), various studies confirm that pattern along elevational gradient are not uniform (Rahbek, 2005; McCain & Grytnes, 2010). This is mainly due to complex biophysical processes that are involved in shaping the fine-scale spatial patterns on mountains. Various elevational diversity patterns has been reported from across the globe, viz., (i) monotonic decline with increasing elevation, (ii) mid-elevation peak, (iii) increasing trend with elevation (iv) low-elevation plateau and then linear decline, and (v) low-elevation plateau with mid-elevation peak (Rahbek, 2005; McCain & Grytnes, 2010). Similarly, the underlying factors that drive the elevational diversity and distribution pattern are diverse and still much debated. Several factors and models have been proposed, which can be broadly categorized as contemporary climate, habitat heterogeneity, evolutionary events, and area or space (Wiens et al., 2007; McCain

&Grytnes, 2010). Variation in patterns among organisms, regions and associated factors makes it difficult to develop a universal model for explaining the diverse trends of biodiversity along elevation (Vetaas et al., 2019). Therefore, studies that are focused on specific taxa or region needs to be conducted to develop more specialized models.

It is widely accepted that apart from ecological factors, biogeographic history such as dispersal, isolation, speciation and extinction events plays an important role in shaping distribution of species (Gutiérrez, 1997; Wiens & Donoghue, 2004). The use of molecular phylogenetic techniques in biogeographic studies aids in understanding such processes in the mountains. Evolutionary hypothesis such as “Vertical speciation” and “Tropical niche conservatism” have been tested to explain distribution pattern of different taxa in the mountain region. Additionally, molecular approaches using DNA sequence data have often aided in proper differentiation of cryptic species assemblages (Burns et al., 2008). Further, the use of molecular sequences also aids in proper systematics of organism which is very important for biogeographic studies (Santos & Amorim, 2007). The DNA bar-coding approaches has helped in discovering cryptic assemblage of several butterfly taxa such as *Astraptes fulgerator* and *Perichares philetes* (Hebert et al., 2004; Burns et al., 2008).Various genes such as nuclear Elongation factor (*EF-1α*) and wingless *(Wg)* are now commonly being used along with cytochrome c oxidase subunit I (*COI*) to understand deep rooted phylogeny of butterflies and their biogeography (Peña et al., 2006). Phylogeny-based studies on species distribution in the mountain region is comparatively less and only handful of literatures in this aspect are available (Willmott et al., 2001; Hall, 2005; Gillespie et al., 2013).

Various faunal groups such as fishes (Fu et al., 2006; Bhatt et al., 2012), amphibians (Fu et al., 2006; Wiens et al., 2007; Smith et al., 2007; Chettri & Acharya, 2020), reptiles (Chettri et al., 2010; McCain, 2010), birds (McCain, 2009; Acharya et al., 2011b) and small mammals (Patterson, 1998; McCain, 2004; Rowe, 2009) has been used as a model taxa for understanding the species richness pattern along the elevational gradient. Among the insects, butterflies are the most studied group (Lawton et al., 1987; Fleishman et al., 1998; Pycrz & Wojtusiak, 2002; Pycrz et al., 2009; Leingärtner et al., 2014). Butterflies are considered important taxa owing to their significant ecological role in ecosystem as pollinators and also as a source of food for many predators. Pollinators are facing a threat of extinction worldwide due to global climate change and anthropogenic activities, resulting in a pollination deficit which might trigger food shortages in the future (Allen-Wardell et al., 1998; Vanbergen, 2013). Biogeographical studies are more important particularly in mountain regions such as the Himalaya where the effects of climate change and anthropogenic pressure are more pronounced as compared to other parts of the world (Singh et al., 2011).

Sikkim is located in the western part of the Eastern Himalaya. Considering its small geographical area (7096 Km^2), diversity of butterflies is very high in Sikkim (689 species representing around 50% of the total species found in the Indian subcontinent; Haribal, 1992). The region is well suited for diversity studies along elevation gradient due to sharp and continuous transition in vegetation and climatic conditions within a very small geographical range. In the Himalayan region, systematic studies on butterflies are scarce (Bhardwaj et al., 2012; Acharya & Vijayan, 2015; Chettri, 2015; Vetaas et al., 2019) and only little is known about butterfly diversity at local and regional scales both qualitatively and quantitatively. Some group of butterflies appears to be highly diversified in Sikkim and is found from as low as 300 m to 5000 m (Haribal, 1992). Several species and subspecies are possibly endemic to the Sikkim Himalaya. Phylogenetic analyses of such butterflies with evaluation of their distribution data would therefore be crucial in order to assign them in proper taxonomic position. Additionally, these groups will form ideal taxa for case studies to ascertain various evolutionary processes that may have shaped the present day distribution of butterflies in the Eastern Himalaya.

1.2 Review of literature

1.2.1 Studies on diversity pattern along the elevational gradient

The variation in number of living organism along spatial and environmental gradients might have been known to the humans since ancient times (Lomolino, 2001). Such knowledge perhaps facilitated the migration of early hunters and gatherers in search of quality environment and food. With the advent of "age of exploration" during the 19th century, naturalists began observing and recording the variability in life forms around the globe (McCain &Grytnes, 2010). Earlier naturalists such as Von Humboldt through the exploration along Mt Chimborazo in Eucadorian Andes, Darwin in Chilean Andes and Wallace in Indonesia noted decrease in diversity of life forms with an increase in elevation (Lomolino, 2001). But it was only during the 20th century attempts were made to explain the diversity pattern qualitatively and quantitatively along the elevational gradient.

The earliest work during the 20thcentury is that of Grinnell and Storer (1924), who found unimodal pattern (mid elevational peak) of richness of various taxa such as bats, nonflying small mammals, breeding birds, amphibians and reptiles. In contrary to previous findings, Grinnell et al. (1930) reported a decreasing pattern of species richness for reptiles and bats and unimodal pattern for nonflying small mammals and birds along the elevational gradient in Northern California, USA. Similarly, Whittaker (1960) also found unimodal pattern along elevation for plants and decreasing trends for insects in Great Smoky mountains in USA. Along the tropical mountains, Terborgh and Weske (1975) and Terborgh (1977, 1985) found a decreasing trend of bird species richness along the Andean elevational gradient. Hence, decreasing trend was thought to be a more generalized pattern for more than 20 years (Stevens 1992), considering that the pattern along elevation mirrors that of latitudinal gradient.

Colwell and Hurt (1994) proposed mid-latitude/elevation peak in species richness. This hypothesis was based on hard boundary effect, popularly known as the mid-domain effect (MDE). However, the mid domain effect is considered to be much controversial as it outweigh the effects of biotic, abiotic and historical factors in shaping the species richness pattern (Dunn et al., 2007; McCain, 2009). Rahbek (1995) analyzed 97 papers (163 examples) to find out whether the data supports the general notion of elevation mirroring the latitude but in contrary found that mid elevation peaks were more common than the linear decrease of species richness. Rahbek (2005) concluded that studies along elevation gradient involving various taxonomic groups have three general patterns viz., monotonic decline, mid elevation peak and linear increase in species richness with elevation. However, other nonlinear decrease in species richness, such as low plateau and low plateau with mid elevation peak also exists (McCain &Grytnes, 2010). These patterns might vary with taxa, regions, and spatial scales (Patterson et al., 1998). The decreasing trend in species richness along the elevation gradient has been documented in reptiles (Chettri et al., 2010; McCain, 2010), birds (Patterson et al., 1998; Blake & Loiselle, 2000) and fishes (Fu et al., 2004; Bhatt et al., 2012). Similarly, mid-elevation peak has been frequently observed in plants (Vetaas & Grytnes, 2002; Oommen& Shanker, 2004); amphibians (Fu et al., 2006; Wiens et al. 2007; Smith et al., 2007); birds (McCain, 2009; Acharya et al.,2011b) and small mammals (McCain, 2004; Rowe, 2009) from different mountains across the globe. Increase in species richness with increasing elevation is perhaps the less commonly observed pattern and has been documented in a few taxa such as ferns in the Central Himalaya (Bhattarai et al.,2004) and amphibians in the Western Ghats (Naniwadekar & Vasudevan, 2007).

Variation in community composition (β diversity) is a critical component of biodiversity that links local (α diversity) and regional (γ diversity) (Whittaker, 1956). Since most the empirical studies on elevational-diversity gradients have focused on species richness or abundance pattern (α/γ diversity), very little is known about the patterns of β diversity along the environmental gradients (Tello et al., 2015). Studies along the latitudinal gradients have shown the decline of β diversity among sites from tropical to temperate region (Qian & Ricklefs, 2007). Studies on beta diversity patterns of birds by Wilson & Schimda (1984) and dung-beetles by Harison et al. (1992) are some of the few pioneering works. Patterns such as decline with elevation (Mori et al., 2013; Tello et al., 2015; Sabaitini et al., 2017), mid-elevational peaks (Mena et al., 2005; Hu et al., 2018; Naud et al., 2019) as well as increasing pattern (Sánchez-Gonález & López-Mata, 2005; Castro et al., 2019)has been recorded for beta diversity along elevation. However, it is certain that the beta diversity significantly increases with increase in elevational distance between the sites (Hu et al., 2017; Jiang et al., 2019).

Harrison et al. (1992) showed that beta diversity may reflect two different phenomena, turnover in species composition or nestedness. Turnover component of beta diversity reflects the phenomenon of species replacement by other species from site to site (Qian et al., 2005). Nestedness, in contrast, occurs when assemblages having fewer species form subsets of those with more species. Baselga (2010, 2013) delineated various statistical models to account for both type of components while considering compositional similarity. Much of the available literature suggests that turnover is the major cause of variation in species assemblages along elevational gradients as a result of abrupt abiotic changes (Flores et al., 2018; da Silva et al., 2018a; Jiang et al., 2019), whereas relatively few studies have found nested structure in species compositional dissimilarity along elevational gradients (Patterson et al., 1996; Presley et al., 2012).

1.2.2 Drivers of elevation-diversity gradients

Researchers have enlisted several factors, processes and models to explain various elevational-diversity patterns. Based on McCain and Grytnes (2010), the potential factors can be categorized into four main types: climatic, spatial, evolutionary and biotic processes.

a. Climatic factors and its derivatives: Climatic factors include various abiotic parameters such as temperature, rainfall, productivity, humidity and cloud cover. Several hypotheses have been proposed to explain the role of climate on distribution of species.

Brown et al. (2004) postulated the metabolic theory of ecology (MTE) which presumes that the higher temperature results in higher energetic lifestyles of organisms thus facilitating faster rates of evolutionary processes which in turn increases the species richness of a region. According to MTE theory, both temperature and biodiversity decreases linearly with elevation. However, it is widely accepted that mid elevational peak in biodiversity is the most commonly observed trend in mountains (Rahbek, 1995, 2005). In those cases, temperature may not directly influence biodiversity pattern but may indirectly act through its influence on productivity. Srivastava and Lawton (1998) has highlighted the relationship of productivity and diversity, and concluded that high productive areas support more individuals within a community and thus, more species. This hypothesis is widely known as "more individual hypothesis" (MIH). Similarly, relationship between precipitation and diversity at both local and regional levels has frequently been documented, but mostly in association with temperature (Hawkins et al., 2003). Precipitation varies along different mountain regimes, hence, the effect may be region specific. While precipitation is considered as major determinant of plant species distributions (Rana et al., 2019) but it act indirectly by influencing the resource availability of the area or habitat in most of the terrestrial animal species (Mc Cain & Grytnes, 2010). O'Brien (2006) highlighted the role of energy (heat/light) in influencing the water availability and termed the phenomena as water-energy dynamics. The energy and water availability are thought to be essential for biological activity that promotes species diversity. Water energy dynamics (WED) has subsequently been demonstrated as better explanation than net primary productivity or more individual hypothesis in explaining species richness pattern of various taxa (Vetaas et al., 2019).

b. Biotic factors: Various biotic factors such as competition, source sink dynamics, ecotone effect, habitat heterogeneity and complexity influence the distribution of organisms along elevation gradient (McCain & Grytnes, 2010). Ecotones represent the areas along the gradient which forms the transition zone between two habitats. These zones are predicted to harbor more number of species possibly due to overlapping ranges and functionality of source sink dynamics (Pulliam, 1988). According to the source sink dynamics model, organism usually occupies an optimal (source) and suboptimal (sink) habitats. Even though the species would not usually survive in suboptimal habitats, the continuous movement of individuals from optimal habitats allows a population to persist indefinitely in the suboptimal habitats (Pulliam, 1988). The ecotonal boundaries represents a sink that receives individuals from the neighboring habitat (source population) resulting into inflation of species richness in these boundaries (McCain & Grytnes, 2010). Diversity in habitat or habitat heterogeneity has also been positively linked with species diversity of different taxa (Bazzaz, 1975; Tews et al., 2004). The monotonic decline in species richness of birds with increasing elevation in Peru was mainly due to the decline in canopy stature and reduced number of plant strata along the elevation (Terborgh, 1977). Similarly, diverse plant communities maintain a diverse assembly of herbivore species along the ecological gradients (Pellissier et al., 2013). Interactions among species such as competition and predation are also important factors which influences the dispersal of organisms (Pianka, 1966). Because of competition on various resources including habitat requirements, species tend to be more specialized and are able to coexist. The predation hypothesis predicts that due to high abundance of predator/prey populations, the population of prey/host is generally kept under control, thus leading to less competition between the prey species. Less competition among species provides an opportunity for intermediate prey to coexist, which in turn supports new predators to increase in overall species richness (Shurin & Allen, 2001).

c. Spatial Factors: Rosenzweig (1992) proposed a species area relationship (SAR) to explain high species richness in the tropics due to availability of larger area. Rosenzweig postulated that the species area relationship act along two scales – regional or global and local scales. In the regional or global scales extinction rate decreases due to the presence of more population in larger area and speciation increases due to potential for formation of barriers. In the local scales, larger area supports more diverse habitat for more species to thrive. Thus along elevation gradient, species-area may function in between these two scales (McCain, 2007). In mountains, species area relationship hypothesis predicts that montane gradient covering more area (e.g. mountain base) should harbor more species (Rahbek, 1997) mostly because of the conical shape of the mountains. Rahbek (1997) showed monotonic decrease in Neotropical bird diversity with increasing elevation in which area accounted for 67-91% of the total variation in species richness. However,some argue that mid-elevation has largest available area (Sanders, 2002; McCain, 2007) resulting in the mid-elevation peak in species richness. However, species-area relationship is not considered as an important driver of species richness pattern along elevation gradient in recent years due to high variability of results among the studies and low explanatory power of area (Sanders, 2002; McCain, 2007).Colwell and Hurt (1994) proposed that the random placement of species' geographic ranges of varying sizes within a region (or domain) bounded by impassable boundaries produces a peak in species richness in the middle of the domain, the phenomena called the mid-domain effect (MDE). The mid domain effect has been well supported by taxa such as mammals (McCain, 2004), birds (Rahbek, 1997) and ants (Sanders, 2002). It has been argued that mid-domain effect might influence richness pattern along latitudinal gradient but it has minimal or no influence at smaller geographical scale, such as elevation gradient (Jetz & Rahbek, 2001; Dunn et al., 2007; Acharya et al., 2011b).

d. Evolutionary factors: Evolutionary processes such as extinction, speciation, biogeographic dispersal and colonization of a species are the ultimate forces that have shaped the present distribution pattern of organisms in the mountains (Gutierrez, 1997; Wiens & Donoghue, 2004). Evolutionary models suggest that areas on mountains that provide optimum condition for speciation, colonization and diversification and minimize extinction risk are usually more diverse. Phylogeny of 137 species (13 genera) of tropical Meso American salamanders revealed the influence of early colonization process in causing the mid elevational peak in species richness (Wiens et al., 2007) The authors found early colonization of mid elevation habitats, and given the equal rate of diversificationof species in all the elevation, more species accumulate in the mid-elevation zone. Similarly, Smith et al. (2007) have linked the colonization history and diversification time and found a mid elevational peak in richness of Middle American tree frogs. According to the study, high species richness at mid elevation was mainly caused by two factors-firstly, the montane clade had tendency to have higher rate of diversification and, secondly, the montane region had been colonized earlier, hence leaving more time for diversification. Thus, the time for speciation and rate of diversification might play an important role in shaping the species richness pattern along the elevation gradient.

The diversity peak at lowland tropical areas of many taxa can be explained by niche conservatism. “Tropical niche conservatism hypothesis” explains that many extant groups originated in the tropical environment and their tolerance to the warmer climate is well conserved ancestral traits (Wiens & Donoghue, 2004). It further explains that the evolutionarily more derived groups are found in the colder environment due to their new acquired adaptability. Willmott et al. (2001) showed relatively higher richness of Neotropical butterflies of the genus *Hypanartia* in the lower elevation due to increased diversification. Higher elevation consisted of relatively few but newly evolved species.

1.2.3Studies on butterflies along the elevational gradient

Insects are known to posses varied trend along the elevational gradients. Many studies have revealed that the species richness of insects peaks at mid elevation (Janzen, 1973; Sanders, 2002; Flores et al., 2018). However, decrease in species richness with increasing elevation is the most commonly reported pattern for majority of the insect groups (Holloway, 1987; Lawton et al., 1987; McCoy, 1990; Sánchez-Rodríguez& Baz, 1995).Lepidoptera, which consists of the moths and butterflies, represents a well studied insect group. Hebert (1980) is one among the few pioneer works in elevational distribution pattern of Lepidoptera. The study reported decreasing species richness and diversity pattern of moths in Papua New Guinea. Similarly, Holloway (1987) found a decrease in species richness of macro-Lepidoptera from lower montane forest to highland forest of the Indo–Australian tropics. Taking butterfly as focal taxa, Sánchez-Rodríguez and Baz, (1995) examined elevational changes in communities in the Sierra de Javalambre of central Spain. The study based on the distribution of 101 butterfly species showed declining trend with maximum abundance and species richness at lower elevation. The harshness of the environmental condition, changes in the vegetation structure and composition, and presumably, sub-optimal resources were considered as the major causes for the decrease in species richness along elevation. Since then, studies from all over the world have examined the elevational trend in diversity of butterflies (**Figure 1.1, 1.2**). Most studies around the globe showed that declining trend is the most common pattern of butterflies along the elevation (Lawton et al., 1987; Vu & Yuan, 2003; Leingärtner et al., 2013; Acharya &Vijayan, 2015) (**Figure 1.3**). Nevertheless mid elevation peak in butterfly species richness has also been reported by few studies(Flieshman et al., 1998; Pycrz & Wojtusiak, 2002; Pycrz et al.,2009; Despland, 2012).Similarly, other patterns were also depicted by some studies, e.g. butterfly species richness followed increasing trend with elevation in Switzerland (Wettstein& Schmid, 1999).

I assessed a total of 33 literatures involving studies on elevational-diversity gradients of butterflies from different mountain regions around the world (**Table 1.1**). Majority of the studies dealt with measures of alpha diversity (species richness, Shannon-Weiner diversity and abundance). A total of 58.06% of the studies reported declining trend, 32.45% showed mid-elevational peak while only9.67% showed an increasing pattern of butterfly diversity along elevation (Figure 1.3). Mid-elevational peaks are often reported to be the most commonly observed pattern for majority of taxa but based on the available literatures, decreasing trend along the elevation is perhaps a more common in case of butterflies. While majority of the studies have focused on alpha diversity, few studies havealso examined beta diversity patterns along elevation mostly explaining the turnover

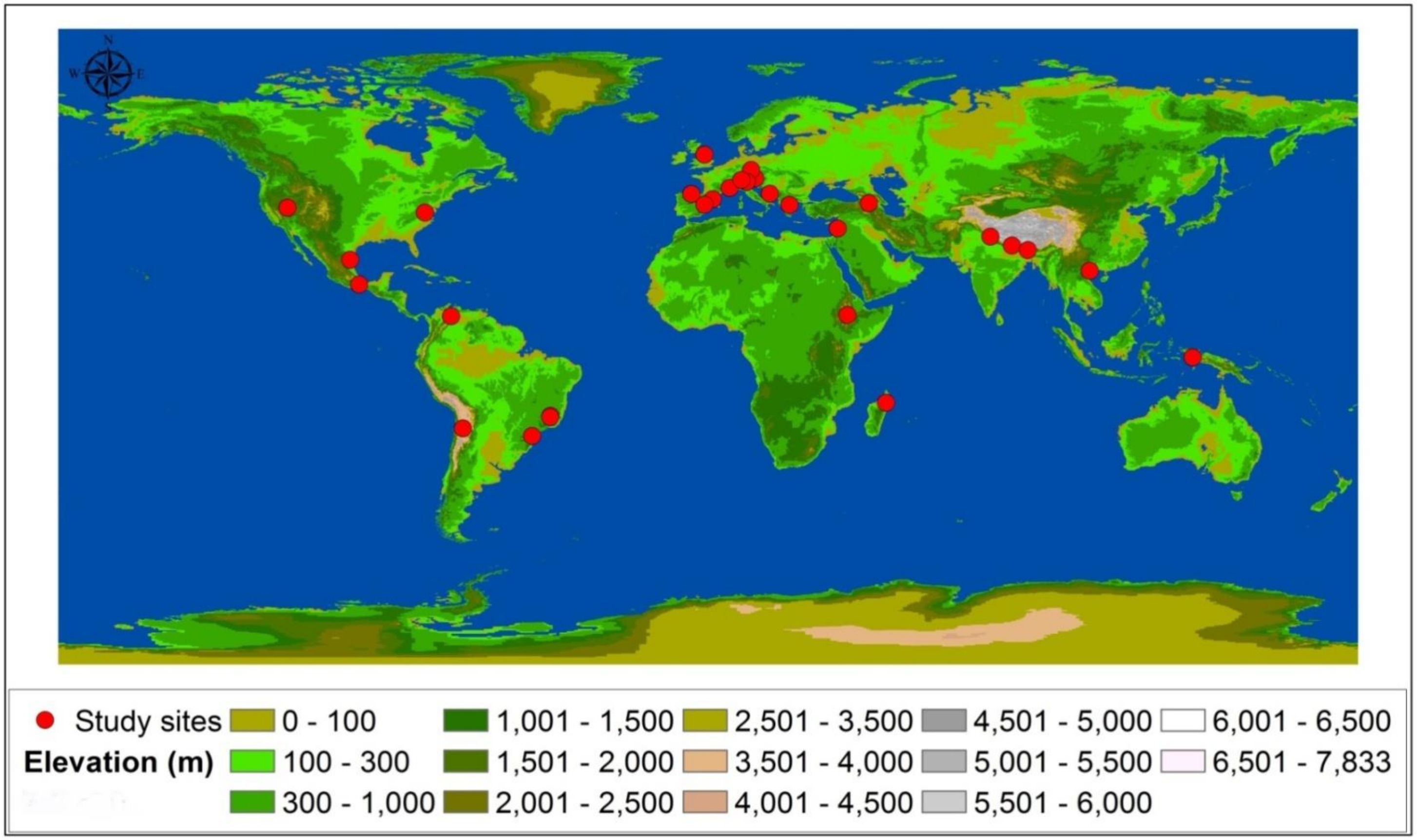


Figure 1.1: Map showing areas where study on elevational-diversity gradient of butterflies has been conducted.

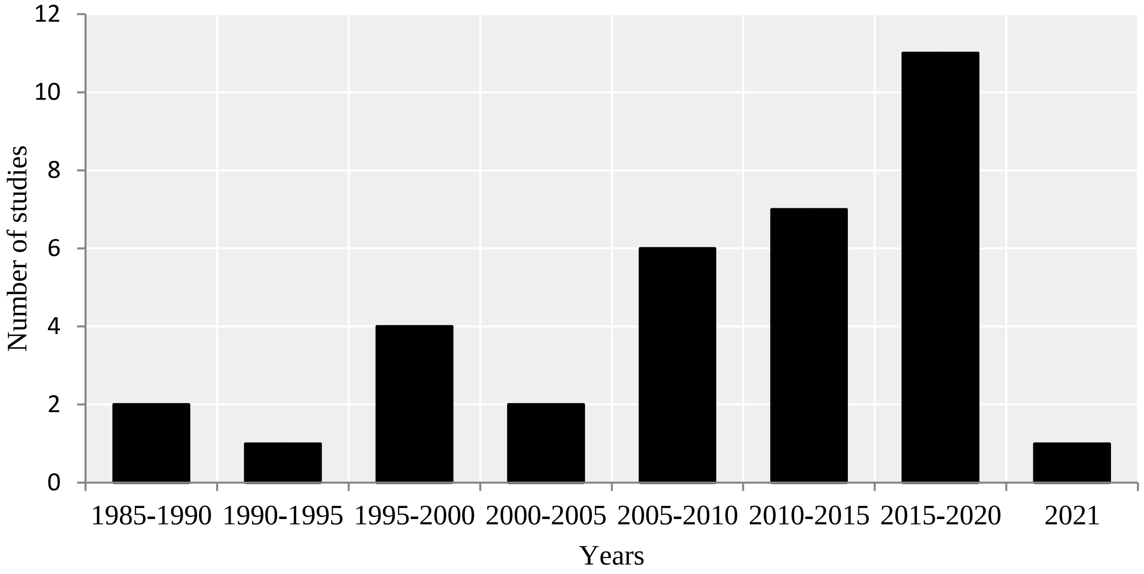


Figure 1.2: Graphical representation of number of studies on elevational-diversity gradient of butterflies during the period between 1985 and 2021 (data is represented at every five year interval except 2021).

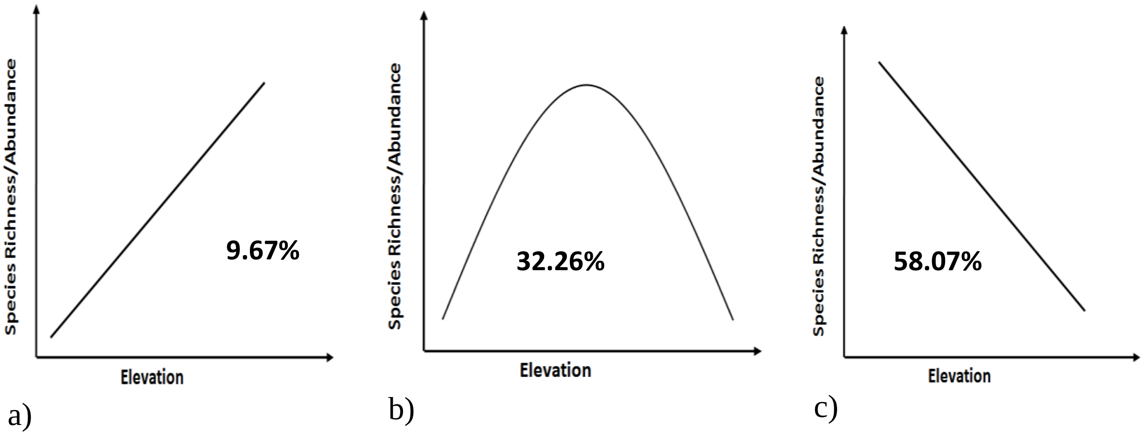


Figure 1.3: Percentage of studies that recorded different patterns of species richness and abundance of butterflies along the elevational gradient form around the world; a) Increasing pattern, b) Mid- elevational peak, c) Decreasing pattern.

Table 1.1: List of studies on elevational-diversity gradient of butterflies from around the world. Details of the α and β patterns, elevational extent of the study and associated factors is also provided.

Sl.No	**Author(s)**	**Mountain transects**	**Elevational extent**	**Community parameters studied**	**α diversity pattern**	**β diversity pattern**	**Associated actors**
1	Lawton et al., 1987	North Yorkshire Moores, England	0-350 m	Species richness	Decreasing trend	-	-
2	McCoy, 1990	Appalachian Mountains, USA	100-1700 m	Species richness	Decreasing trend	-	-
3	Sánchez-Rodríguez & Baz, 1995	Camarena de Sierra, Spain	1100-2000 m	Species richness, abundance	Decreasing trend	-	-
4	Guiterrez,1997	Picos de Europa, Spain	200 - 2600 m	Species richness, abundance	Mid elevation peak	-	Biogeographic affinity
5	Fleishman et al., 1998	Toiba Range, USA	1917 - 3272 m	Species richness	Decreasing trend	-	Rapoport rule
6	Wettstein & Schmid, 2001	Northeastern Switzerland	800–1400 m	Species richness, abundance	Increasing trend	-	Vegetation structure
7	Lees, 1999	Madagascar		Species richness	Mid elevation peak	-	-
8	Pyrcz &Wojtusiak, 2002	Monte Zerpa, Venezeuala	2250-3025 m	Species richness, abundance	Mid elevation peak	-	-

9	Vu& Yuan, 2003	Tam Dao National Park , Vietnam	200-1000 m	Shannon diversity, species richness, abundance	Decreasing trend	-	Habitat changes
10	Uniyal, 2007	Great Himalayan Conservation Landscape, India		Shannon diversity	No definite trend	-	-
11	Joshi & Arya, 2007	Nanda Devi Biosphere Reserve, Western Himalaya, India	2000-3050 m	Shannon diversity, species richness, abundance	Decreasing trend	-	-
12	Bhusal&Khanal, 2008	Eastern Siwalik, Himalaya, Nepal	250-1150 m	Species richness	Decreasing trend	-	-
13	Pyrcz&Wojtusiak, 2009	Nudo de Pasto, Andes	1600-2600 m	Shannon diversity, species richness, abundance	Increasing trend	-	-
14	Levanoni et al., 2011	Mt Hermon, Northern Israel	500-2200 m	Species richness	Mid elevation peak	-	NDVI
15	Stefanescu et al., 2011	Catalonia, Mediterranean, Spain	0-1930 m	Species richness	Mid elevation peak	-	Climate and Anthropogenic factors
16	Mihoci et al., 2011	Mt. Biokovo, Croatia	243-1762 m	Shannon diversity, species richness, turnover	Decreasing trend	Increase in turnover	
17	Bhardwaj et al., 2012	Tons Valley, Western Himalaya, India	900-3500 m	Species richness, abundance	Decreasing trend	-	Temperature/ Humidity/ fire and livestock abundance

18	Despland et al., 2012	Northern Chile	3000-4850 m	Species richness, turnover, phenology	Mid elevation peak	Increase in turnover	Water energy hypothesis
19	Wagner et al., 2013	Fivhtelgebirge, Germany	340–750 m	Species richness	Mid elevation peak	-	Habitat
20	Leingärtner, 2014	Berchestesgardene, Germany	600-2000 m	Species richness, abundance, trait assemblages, Phylogenetic relatedness	Decreasing trend	-	Flower cover and temperature
21	Carneiro et al., 2014	Cartuva Mountains, Brazil	1000-1860 m	Species turnover	-	Increase in turnover	-
22	Acharya &Vijayan, 2015	Teesta Valley, Eastern Himalaya, India	300-4700 m	Shannon diversity, species richness, turnover	Decreasing trend	Increase in turnover	Temperature and Actual Evapotranspiration
23	Chettri, 2015	Dozngri trekking trail, Eastern Himalaya, India	1780-2350 m	Shannon diversity, species richness	Decreasing trend	-	-
24	Gallou et al., 2017	Isere alps, France	200-2700 m	Species richness	Decreasing trend	-	Temperature/ Habitat Variables/ Anthropogenic disturbances
25	Kaltsas et al., 2018	Olympus and Rhodopes , Greece	500-2600 m	Species richness, abundance, beta diversity, functional diversity	Decreasing trend	-	Environmental filtering
26	Jemal & Getu,	Menagesha-suba,	2220-3330 m	Shannon diversity,	Decreasing	Increase in	-

	2018	Ethopia		species richness, abundance, turnover	trend	turnover	
27	Meléndez-Jaramillo et al., 2019	Cerra bufa el Diente, Mexico	553-1085 m	Species richness, density	Decreasing trend	-	-
28	Zarikian et al., 2019	Mt Tsaghkunyats, Armenia	1650-2814 m	Species richness, abundance	Mid elevation peak	-	-
29	Pires et al., 2020	Serra do Cippo, Brazil	800-1400 m	Specie richness, abundance, turnover	Decreasing trend	Increase in turnover	Temperature and plant richness
30	Shrestha et al., 2020	Manand District, Nepal	1600-3500 m	Species richness	Increasing trend	-	-
31	Beirão et al., 2021	Serra do cippo, Brazil	822-1388 m	Species richness, abundance, turnover	Decreasing trend	Increase with elevation	Temperature, Precipitation, plant species richness
32	Fontana et al., 2020	Mazia Valley, Italy	1000-2500 m	Species richness, turnover, nestedness	Mid elevation peak	Increase in turnover , decrease in nestedness	-
33	Popović et al., 2021	Galičica Mountain, Macedonia	689-2234 m	Species richness, turnover	Mid elevation peak	-	Area and productivity

component. In all the studies examined, species turnover has been reported to increase significantly with increasing elevation. Fontana et al. (2020) showed increase in turnover rate of butterflies but decrease in nestedness components along the elevation. The studies have outlined several climatic and habitat variables such as temperature, precipitation, productivity, plant species richness, and flower cover, etc as the determinant of butterfly diversity pattern (both alpha and beta diversity). Similarly, area was the major determinant of richness of butterflies along the elevational gradient in Galičica Mountain, Macedonia (Popović et al., 2021). Anthropogenic disturbances are also known to influence species richness pattern of butterflies in the mountain region (Gallou et al., 2016; Stefanescu et al., 2010).

Many explorers and researchers have studied butterflies of the Himalayan region in the past. One of the earliest mentions of butterflies of the Himalaya can be found in the book ‘Himalayan Journal’ by J.D Hooker published in 1855. Since then, several studies on butterflies have been conducted but majority of them are focused on taxonomy and species exploration. The ecological studies on butterflies including assessment of the species richness pattern along the elevation remains poorly addressed. To my knowledge, a total of seven studies on butterfly elevation-diversity gradient have been conducted till date in the Himalayan region (**Table 1.1**).Among these studies, five have reported the decreasing trend of butterfly richness while two found increasing trend along the elevation. The study of Acharya and Vijayan (2015) remains one the most robust work conducted till date from the Eastern Himalayan region. The study was conducted along large spatial extent coveringabout 4000m elevation range and subsequent models of richness and abundance were tested. The study found declining trend in butterfly species along the elevation gradient with a hump at 1000 m elevation. While various biotic and abiotic factors were correlated with the species richness, mean annual temperature and actual evapotranspiration remained to be most important variables.

1.3 Research gaps

Diversity and distribution patterns of organisms along the elevational gradient around the world has been explored extensively in the last two decades(Gaston & Blackburn, 2000; McCain, 2007; Smith et al., 2007; Weins et al., 2007; Kumar et al., 2009; Li et al., 2009; Wu et al., 2013a; Rana et al., 2019). Proposing a universal model for explaining diversity gradients along the elevation has been rather difficult because there are considerable variation in the patterns and process across mountains, biogeographical locations and taxa considered. Therefore, to develop more specified models, studies on specific taxa or region is necessary. In case of butterflies, most of the research on elevational-diversity gradient is available from temperate regions, mostly from Europe but very few studies are reported from species rich tropical regions (Vu& Yuan, 2003; Carnerio et al., 2014; Pires et al., 2020). Even when compared to taxa such as mammals (McCain, 2005), birds (McCain, 2009), and reptiles (McCain, 2010), studies on butterflies are relatively less. Further, most of the studies have only considered species richness (α diversity) while only few have focused on β-diversity pattern and range size distribution (Despland et al., 2012; Carnerio et al., 2014; Micho et al., 2011; Fontana et al., 2020).

In the Himalaya, biogeographic study on butterflies has been mostly conducted on high elevation transects and along a small spatial extent (<2000m) (except Bhardwaj et al., 2012 and Acharya &Vijayan, 2015). Further, only few have considered environmental or spatial factors as potential determinants to understand the resultant pattern. Nonetheless, the diversity trend can vary at local and regional scales both quantitatively and qualitatively (Rahbek, 2005; McCain & Grytnes, 2010). Hence, it is important to explore other elevation gradients to explore the generality of the pattern even in the same region. Additionally, several studies have shown that trends in different ecological or taxonomic groups within same taxa varies considerably (Oommen & Shanker, 2005; Beck & Chey, 2006; Fu et al., 2006, Wu et al., 2013b; Hu et al., 2017; Zhou et al., 2019, Chettri & Acharya, 2020). Assessment of diversity pattern along elevation while considering different butterfly groups have not been consideredin the previous studies in the Himalaya and elsewhere. Lastly, evolutionary mechanism that shapes distribution pattern of butterfly and relationship of several Himalayan butterfly species remains poorly understood.

1.4 Objectives

The present study was conducted to address some gaps in research of butterflies along the elevational gradient. The broad aim of this study was to understand the distribution pattern of butterflies along an elevation gradient with the following specific objectives:

1. To analyze and explain species richness pattern, range size distribution and turnover rate of butterflies along elevation gradient in Rangeet valley in Sikkim Himalaya.
2. To understand the potential factors influencing the elevational pattern of butterflies.

3. To explore the abundance trend of wide ranging butterfly species along elevation gradient.
4. To understand the distribution pattern and phylogeny of some closely related species.

1.5. Organization of the thesis

The thesis has a total of seven chapters which is organized as follows:

1. Chapter 1 provides a brief introduction of this study. Here I review literatures that have studied the elevational pattern of biodiversity in different mountains around the world. The chapter also provides a summary of research gaps, based on which the objective of the study was formulated.
2. Chapter 2 provides the overview of the study area. In this chapter I first provide brief details about the Sikkim Himalayan region. I then discuss the topography, climate and vegetation structure along the elevation in Rangeet Valley.
3. Chapter 3 deals with understanding the pattern of species richness and density of butterflies (total as well as ecological sub-groups) along the elevation gradient in Rangeet Valley. The patterns are described, the role of underlying factors presented and discussed in this chapter.
4. In Chapter 4 the elevational beta diversity pattern of butterflies of Rangeet Valley is provided. I also assessed various underlying factors for the resultant pattern.
5. Chapter 5 is based on the study of elevational range size distribution of butterflies and test of the Rapoport elevational hypothesis. The chapter also deals with the

density pattern of large range species. Here, I also test the relationship of density and range size of butterflies.

6. Chapter 6 deals with the phylogeny of Genus *Lethe* (Nymphalidae: Satyrinae). I estimate the time of diversification of the group and relate its evolutionary history to the current elevational distribution pattern of *Lethe* butterflies.
7. Chapter 7is the concluding chapter of the thesis. Here I summarize the findings of this study and also discuss the potential outcome of the study, especially in formulating conservation strategy for butterflies in Sikkim.

CHAPTER 2

STUDY AREA

2.1 Sikkim Himalaya: a brief overview

The Himalaya constitutes a stretch of mountain range in Asia that separates the Indian sub-continent from the Tibetan Plateau. The Himalayan range stretches from the ridges beyond Nanga Parbat(Pakistan) in the east to Namcha Barwa (China) in the west, covering a distance of approximately 2500 km and has a width of about 240-350 km (Roy & Purohit, 2018). The entire stretch expands across the nations of Afghanistan, Pakistan, India, Nepal, Bhutan, Bangladesh, China and Myanmar.The range harbors many of the world’s highest mountain peaks such as Mt. Everest (8848.86 m), Mt K2 (8611 m), Mt Khangchendzonga (8686m), etc. Abrupt rise in elevation (60-8848.86 m) and complex topography of the Himalaya creates a range of climatic regime from hot tropical conditionin the lowlands, cool temperate in the mid hills to cold alpine tundra in the higher elevation. Gradation of climate along the elevation offers unique niches for diverse form of flora and fauna to thrive in the region. It is estimated that over 10,000 species of plants, 270 fishes, 980 birds, 300 mammals, 175 reptiles and105 amphibians are found in this region. High diversity and endemism of living organisms and its vulnerability to threat makes the Himalaya one among the 36biodiversity hotspots of the world (CPEF, 2020).

The vast mountain range of the Himalaya has broadly been divided into Western, Central and the Eastern Himalaya. The Eastern region represents the mountain range stretching across central Nepal, Bhutan, northeast India, Yunnan in China and northern Myanmar. It covers an area of approximately 524,190 Km^2.The Eastern Himalaya comprises of steeper elevational gradient than its western counterpart. During monsoon, the region receives more rainfall from the moisture laden South-East monsoon winds that originates from the Bay of Bengal and South China Sea. As a result, the moist Eastern Himalaya is comparatively more biodiverse than the Western Himalaya. The region includes 25 of the Global 200 Ecoregions (Olson & Dinerstein, 2002), Endemic Bird Area (Stattersfield et al., 1998) and several centers for plant diversity (WWF/IUCN, 1995). The Eastern Himalayaencompasses species from Palearctic realm, Indo-Malayan realm and Sino-Japanese region (CEPF, 2020).

Sikkim (27^{O}03’ to 28^{O}07’ N and 88^{O}03’ to 88^{O} 57’ E) is a small northeastern state of India that lies in western extremities of the Eastern Himalaya. The state is characterized by steep mountain terrain that runs from the lowest elevation of about 300m to 8586m, the height of Mt. Khangchendzonga. Two major rivers, Teesta and Rangeet, originate here carving the hills and mountains into deep valleys and gorges, and finally merges with river Brahmaputra. The state is surrounded by three ranges; Singalila range on the west, axis of Trans Himalaya and Tibetan plateau in the north and Chola range in the north-east. These natural barriers act as an international boundary that separates Sikkim with Nepal, Bhutan and Tibetan Autonomous Region (China) respectively. These ranges also play a prominent role in influencing the atmospheric circulation and climate of Sikkim and surrounding areas (Rawat & Tambe, 2011). Sikkim shares its southern boundary with the hill districts of West Bengal, India. Sikkim Himalaya, due to the steep rise in elevation exhibits a rapid transition of eco-climatic zones within relatively short distance. The annual temperature ranges from sub-zero during the winter to 28^{O} C in the summer while annual precipitation ranges from 2700-3200 mm. Temperature decrease linearly with elevation at the rate of -0.5^{O} C per 100 meters (Dewan et al.,2021). The lower and middle elevation region receives high rainfall while precipitation in high elevation sites remains in form of snowfall for most of the year. Due to its close proximity to Bay of Bengal and Tibetan plateau,the region shows affinity to the tropical moist forests in the south and dry alpine steepe in the northand such transition is witnessed within a distance of around 100 km (Rawat& Tambe, 2011). Although, most of the biodiversity components in Sikkim represent the Eastern Himalayan element, species having affinity to western Himalaya can also be found here. This unique feature of Sikkim makesit one of the most biologically diverse regions in India irrespective of its small geographical area (7096 km^2).

Sikkim is bestowed with about 40% of the total biodiversity found in India (Acharya &Sharma, 2013). Sikkim consist about 4458 species of flowering plants out of the estimated total 18,000 species reported form the country. The non flowering plant includes 506 Lichens, 480 pteridophytes and 17 species of gymnosperms. A total of approximately 5892 species of arthropods are found in Sikkim that includes77species of odonates and about 689 butterflies (Haribal, 1992; Chandra, 2011; Payra & Bhutia, 2017). The vertebrates are represented by 50 fishes, 50 amphibians, 88 reptiles, 574 birds and 169 species of mammals(Acharya &Sharma, 2013).

The existence of significant biodiversity wealth is supported by the presence of high percentage of natural habitats. The total forest cover of Sikkim is 3378.49 km^2, which is about 47.11% of the total geographic area of the state (FSI, 2019). Altogether, 46.93%(3330.28 km^2) of the state's geographical area (7096 km^2) lies under the Protected Area Network which comprises one National Park and seven Wildlife Sanctuaries. Outside protected areas, traditionally managed agro-forestry systems are known to retain high biodiversity conservation value (Sharma et al., 2020).

2.2 The Rangeet Valley

2.2.1 Location and Topography

Sikkim Himalayan region consist of mountain landscape that is traversed by the River Teesta and several of its tributaries through series of sub-parallel valleys. The Rangeet Valley (**Photo plate 2.1**) represents a vast stretch of riverine watershed area that lies in west and south districts of Sikkim drained by River Rangeet and its tributaries. The north-south ridge that runs through central Sikkim separates the Rangeet with the Teesta Valley. The Rangeet river originates in the high altitude glaciers of Mount Kabru (7,412 m) at the southern flank of the Khangchendzonga Massif located in the west Sikkim district (Vezzoli et al., 2017). From the ice feed glaciers, the river flows south ward cutting through deep gorges and are fed by many tributaries along its downstream course. Major tributaries of Rangeet riverare the Prek Chu, Chokhurang Chu, Kalej Khola and Ramam Khola. The Rangeet river finally merges with the river Teesta near Melli at Sikkim-West Bengal border at around 300 m elevation.

Around 40% of the entire Rangeet Valley basin is surrounded by the high elevational mountain. The upper and the middle basin chiefly fall in the western district and is

Photo plate 2.1: a) Google Earth view Sikkim (marked with yellow border) in the stern Himalaya,b) Closeup view of Rangeet Valley through Google Earth showing important land marks,c) Khangchendzonga Mountain Range,d) Closeup view of Mt. Khangchendzonga,e) Panoramic view of Rangeet Valley form, Deorali (4000 m).

characterized by high ridges and deep narrow valleys. Slopes of these landscapes are steep with a sharp elevational gradient. The lower basin that mainly lies in the Southdistrict is characterized by wide and open valleys. The entire catchment of Rangeet river stretch over 80km in length and 2200 km^2 in area (Vezzoli et al., 2017). The elevational range fromthe lowest point in the valley to the highest peak ranges from 300 m to 8586 m (the height of Mount Khangchendzonga).

2.2.2 Climate

The Rangeet Valley experiences high variability in climatic condition along its elevational gradient. The climatic data provided here is extracted from climatologist at high resolution for the Earth's land surface areas (**Figure A.1**) (CHELSA;Karger et al., 2017 a,b).The temperature decreases linear with the elevation while the precipitation shows a hump shaped pattern peaking at mid elevation. The lower valley (below 1000m) experiences a warm tropical climate with an annual temperature of 17 to 25^{O} C and precipitation of1190-1913 mm. The relative humidity of this area ranges between 63-64%. The summers in lower elevation is hot and winters are cool and dry. The climate between 1000-2000 m elevation is of high hill type where the mean annual temperature and precipitation ranges between 10.33-21^{O} C and 2052.74-2272.28 mm respectively. This elevational zone represents the transition point between sub-tropical to temperate climatic condition. The relative humidity in this zone increases to about 87% due to high precipitation. The maximum precipitation is received during the summer months. The zone lying in between the elevation of 2000-2800 m is cool and humid. The annual temperature of this zone is between 13.3 to 9.4^{O}C while the precipitation ranges between

2345.48-2292.93 mm and is the most humid region along the valley. The elevational zone between 2800-3300 m has cool summers and chilling winters. The annual temperature in this elevation zone is about9.4-4.6^{O}C. The temperature in the uppermost edges of this zone reaches below 0^{O}C. While average annual precipitation is high in this zone (2094.18-2292.93mm), the rainfall is mainly received during the summer months. During the winter season, precipitation is received in the form of snowfall. Moving upwards, 3800-5000m is characterized by sub-alpine climate which is relatively cold throughout the year. The annual mean temperature in this zone falls between 4.6-0.6^{O} C. The region receives very less rainfall even during the peak summers while the precipitation remains as snow for most of the time. The annual precipitation in this zone ranges between 291 - 1000 mm.The elevation above 4500m represents the alpine region wherein the temperature remains sub-zero and receives no/very less rainfall. The high peaks (mountain top) remains covered by snow throughout the year.

2.2.3 Vegetation type

Various classification of forest types of the Himalayas exist in the literature (Hooker 1854; Champion & Seth, 1968; Haribal, 1992). Here we describe the forest type based on elevation following Haribal (1992) and Acharya and Sharma (2013) (**Photo Plate 2.2**). The forest types can broadly be classified into:

i. Tropical semi-deciduous forests (300-900 m): The tropical forest occurs at low elevation zone of Rangeet valleyespecially at the border betweenSikkim andWest Bengal state of India. Deciduous trees such as *Shorea robusta, Duabanga grandiflora* and *Tectona grandis*are mainly dominant species in this forest type. Other trees species such as *Terminalia belerica*, *Garuga pinnata*,*Amoora spectabilis, Bombax cebia*, *Castanopsis indica, Chukrasia tabularis*, *Bischofia javanica*, *Pandanus furcatus*, etc., occursin this elevation zone. Some the forested areas in lower valleys (especially in Kitam Bird Sanctuary) are dominated by *Pinus roxbhurgii*. Secondary growths are represented by various species of *Strobilanthes*, *Polygonum*, *Barleria*, etc. The forest cover in this elevation has been tremendously altered due anthropogenic activity such as building of dense road networks, pharmaceutical industries and hydro power projects. However, remnant patches of original forest still exist in some areas. Kitam Bird Sanctuary (6 km^2 area) along the Rangeet River basin is the only protected area in this elevation zone.

ii. Tropical moist and broad-leaved forests (900-1800 m): Forest within this elevation zone is of mixed nature. Trees such as *Schima wallichii*, *Castanopsis indica, Castanopsis tribuloides*, *Michelia cathcartii*, *Alnus nepalensis*, *Terminalia myriocarpa*, *Macaranga denticulata*, *Magnolia hodgsonii*,*Ostodes paniculata*, etc., are commonly found here. Plants such as *Maesa* sp, *Bidens pilosa*, *Girardinia palmata*, *Artemisia* sp, *Boehmeria* sp, *Smilax* sp, etc consists of major secondary vegetation. The tree ferns, orchids and *Rhapidophora*sp are also represented in this forest type.

iii. Temperate broad-leaved forests (1800-2800 m): Forest in this elevation ischaracterized by closed canopy of broadleaved trees covered by mosses and other epiphytes. Oak trees belonging to genus *Castanopsis*, *Quercus*and *Rhododendron arboreum* are dominant in this elevation. Other trees found here includespecies of genus *Magnolia, Michelia, Ilex, Cinnamomum, Betula*, etc. Undergrowth consists of *Deberegesia* sp, *Utrica* sp,*Osbeckia* sp,*Melostoma* sp etc. Bamboos of the genus

Arundinaria are also commonly found here. Forests of this elevation are mostly undisturbed in Sikkim as majority of the protected area lies in this belt. The oak forest in west district forms the outer most boundary of Khangchendzonga National Park.

iv. Temperate coniferous forests (2800-3800 m): Forest in this elevation belt ismostly dominated by conifer trees such as *Tsuga dumosa*, *Abies densa*and *Picea smithiana*. Species such as *Larix griffithiana, Taxus walichiana, Acer caudatum, Rhododendron arboreum, Rhododendron campanulatum*, *Rhododendron grande* and *Betula utilis* are also found in this elevation. Undergrowth vegetation is chiefly dominated by *Berberis*sp, *Ilex*sp, *Rubus*sp, *Spiraea*sp, *Viburnum*sp, etc. The common secondary outgrowth includes *Impatiens* sp, *Geranium* sp, etc.

v. Sub-alpine vegetation (3800-4500m): With gradual increase in elevation, adverse climatic condition impedes the growth of trees. Tree line in west Sikkim is located at about 4000m elevation. Several varieties of *Rhododendron* are commonly found here but remains poorly developed throughout the year due to extreme climatic conditions. Other plant species includes *Potentilla* sp, *Anemone* sp, *Primula* sp, *Ligularua* sp, *Pedicularis*sp, etc. that blooms during April to August when climatic conditions are favourable.

vi. Alpine zone (>4500 m): The zone represents high Himalaya which remains covered under the snow almost throughout the year. The vegetation is represented by typical cold desert plants which only blooms duringspring time. Plants of genus*Meconopsis*, *Sedum*, *Potentilla*, *Saussurea*, *Pedicularis, Iris, Corydalis, Poa*,etc occurs here. *Rheum nobile*, a gigantic rhubarb and medicinally important caterpillar fungus *Ophiocordyceps sinensis* also occurs in this region.

Tropical semi-deciduous (300-900 m)

Tropical moist broad leaved (900-1800 m)

Temperate broad leaved (1800-2800 m)

Temperate coniferous (2800-3800 m)

Sub-Alpine Vegetation (3800-4500 m)

Alpine (> 4500 m)

Photo plate 2.2: Photographs of different vegetation types observed along the elevational gradient in Rangeet Valley Sikkim, Eastern Himalaya

2.3 Selection of study sites

The present study was conducted along the elevation gradient ranging from 300m to 3300m in the Rangeet Valley (**Table 2.1; Figure 2.1**). Sampling in the high elevation area above 3300m was logistically not viable due to extreme climatic conditions. Hence, four major vegetation types were covered in the study namely Tropical semi-deciduous forest, tropical moist and broad-leaved forests, temperate broad-leaved forests and temperate coniferous broad-leaved forests. Entire elevational zone (3300m, considered for the study) was divided into 16 vertical elevational zones. The elevational distance between the two consecutive zones were 150-200 m. In each zone, suitable forest sites were identified owing to their accessibility and feasibility for field sampling. Before selecting the sites, I made sure that the areas had good percentage of forest cover and had minimal anthropogenic disturbances. A transect of 1000m length were established in each of the zonefor sampling butterflies and vegetation. In each transect I established 10 permanent circular points (5m radius) for butterflies, 10 (10x10m) quadratic plots for trees and 20(5x5 m) plots for shrubs (details of the sampling techniques is provided in Chapter 3).

Table2.2: Details of butterfly and vegetation sampling sites along the elevational gradient in Rangeet Valley,Sikkim Eastern Himalaya.

Study Sites	**Area**	**Vegetation**	**Elevation**	**Latitude**	**Longitude**
Kitam	T1	TSDF	3500	27° 06' 47.18" N	88° 21' 40.45"
Phursachu	T2	TSDF	500	27° 18' 14.44" N	88° 18' 14.44"
Legship	T3	TSDF	600	27° 16' 33.79" N	88° 16' 08.56"
Rangeet Bridge	T4	TSDF	800	27° 17' 56.74" N	88° 18' 20.50"
Hingdam	T5	TMBF	1000	27°16'45.29"N	88°16'49.33"E
Rimbi	T6	TMBF	1300	27° 18' 51.76" N	88° 11' 49.82"
Tashiding	T7	TMBF	1450	27° 18' 43.64" N	88° 17' 55.69"
Lasso	T8	TMBF	1600	27° 19' 44.93" N	88° 17' 21.17"
Khecheopalri	T9	TMBF	1750	27°21'7.57"N	88°11'12.41"E
Yuksom	T10	TBLF	1900	27° 21' 51.68" N	88° 12' 52.88"E
Pha Khola	T11	TBLF	2100	27°23'44.16"N	88°13'1.30"E
Sachen	T12	TBLF	2300	27°24'50.07"N	88°11'49.12"E
Gaikhurey	T13	TBLF	2500	27°25'36.54"N	88°11'28.13"E
Bakhim	T14	TBLF	2700	27°25'41.30"N	88°11'10.98"E
Merek	T15	TBCF	2900	27°25'52.84"N	88°11'8.33"E
Tshoka	T16	TBCF	3100	27°26'58.02"N	88°10'43.29"E

TSDF (Tropical semi-deciduous forest); TMBF (Tropical moist and broad-leaved forests); TBLF Temperate broad-leaved forests; TCBF (Temperate coniferous and broad-leaved forests)

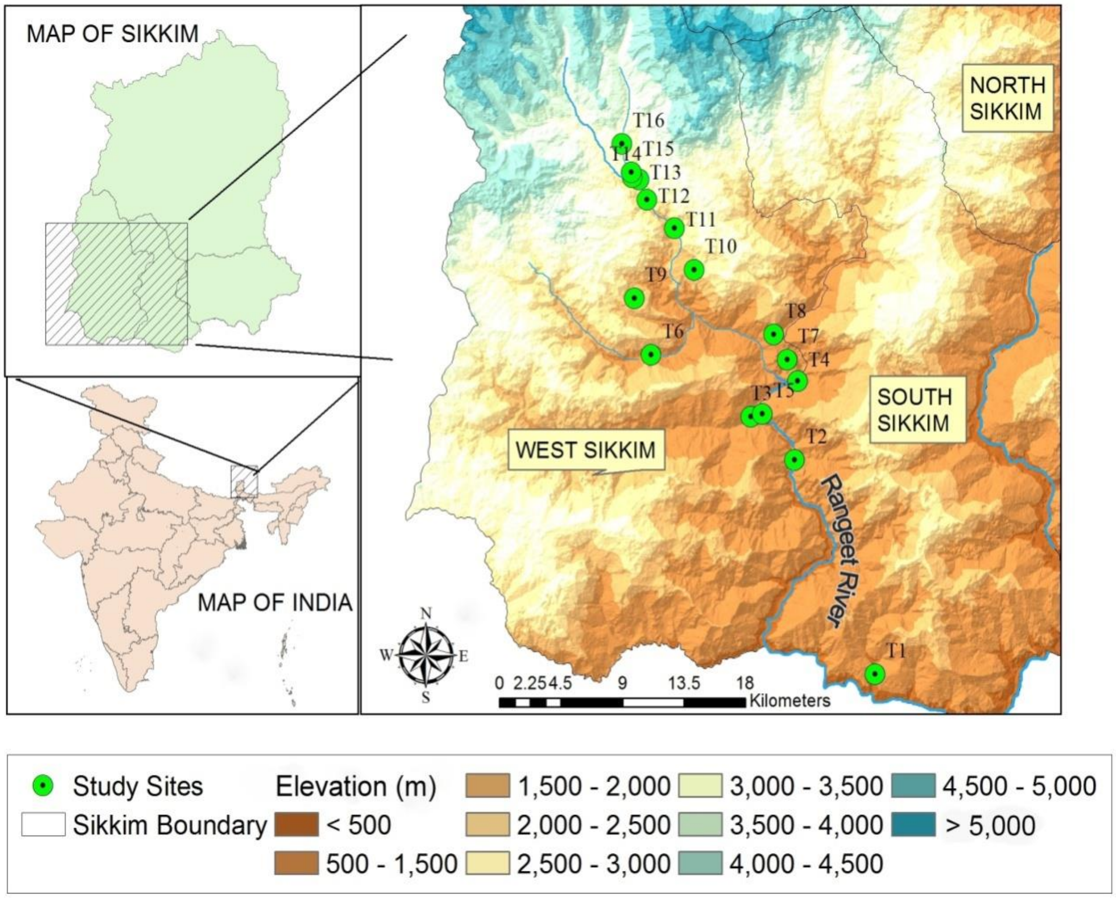


Figure 2.1: Map showing the locations of the 16 sampling transects along the elevation gradient in Rangeet Valley, Sikkim, Eastern Himalaya.

CHAPTER 3

SPECIES RICHNESS AND ABUNDANCE PATTERN OF BUTTERFLIES ALONG THE ELEVATIONAL GRADIENT

3.1 Introduction

Species richness and abundance of living organisms shows marked variation across spatial gradients. As discussed in Chapter 1, species richness and abundance of different taxa follows decreasing, mid-hump or increasing trend along the elevational gradients (Rahbek, 2005). Factors that determine the richness or abundance pattern can be broadly grouped into contemporary climate, habitat heterogeneity, evolutionary events, and area or space (McCain & Grytnes, 2010). Among invertebrates, butterflies serve as a suitable model organism to test various biogeographic hypotheses because they are easy to identify and monitor, and are relatively responsive to environmental changes (Luoto et al., 2006). Studies from around the world have reported all the three patterns of richness and abundance of which monotonic decline is the most commonly observed pattern for butterflies (Sanchez-Rodriguez & Baz, 1995; Wettstein & Schmid, 1999; Pycrz & Wojtusiak, 2002; Kumar et al., 2009; Despland et al., 2012; Leingärtner et al., 2014). The studies have recognized climatic, spatial and habitat variables as well as anthropogenic impacts as a potential driver of species richness and abundance of butterflies. The disparity in the observed trends and perceived process are possibly due to the difference in climatic regime and topography of the mountains and variation in the spatial extent considered for the study (Rahbek, 2005; Shuai et al., 2017). Therefore, regional specific studies are necessary to be conducted in order to develop more specialized models of elevational diversity gradients.

Trends in diversity of different butterfly sub-groups might differ along the elevation. Most of the taxa taken into consideration can be grouped into meaningful ecological sub-groups (Oommen & Shanker, 2005). Previously, ecologist have studied diversity trends of taxa such as plants, moths, mammals, birds, and amphibians by categorizing them according to their range size, biogeographic affinity, taxonomic categories, and feeding guilds (Oommen & Shanker, 2005; Beck & Chey, 2006; Fu et al., 2006; Wu et al., 2013b, Hu et al., 2017; Zhou et al., 2019, Chettri &Acharya, 2020). Different ecological or phylogenetic groups within the same taxa may have different diversity patterns and their responses to abiotic and biotic factors may vary. For example, large-range species due to their wide environmental tolerance may only be affected by geographical constraints, whereas small-range species being more specialized in their niche are influenced by environmental factors (Fu et al., 2006; Wu et al., 2013b; Hu et al., 2017). Additionally, small-range species being often rare as compared to the large-range species might be more vulnerable to climate change (Elsberry et al., 2018). Similarly, as per the biogeographic origins, species having tropical affinity are mostly narrowly distributed while temperate species shows wider distribution and are more environmental tolerant (Li & Feng, 2015; Zhou et al., 2019). Larval host plant specificity of Lepidoptera is also thought to influence elevational distribution pattern. The elevational niche-breadth hypothesis predicts that the diet breadth of herbivores increases with increasing elevation (Rasmann et al., 2014). However, no concrete evidence exists for such an assumption (Brehm et al., 2007).

In the Himalaya, studies on the elevational distribution patterns of various taxa (Vetaas et al., 2019 and references therein), including plants (Bhattarai et al., 2004; Oommen & Shanker, 2005;Acharya et al., 2011b; Sharma et al., 2019), fishes (Fu et al., 2004; Bhatt et al., 2012), amphibians (Fu et al., 2006, Chettri & Acharya, 2020), reptiles (Chettri et al., 2010), birds (Acharya et al., 2011a; Wu et al., 2013a), and mammals (Wu et al., 2013b; Hu et al., 2017) has been carried out. While butterflies of Himalayan region have been subject of taxonomic research for naturalist since 1800s, biogeographic studies remain scanty till date (Bhardwaj et al., 2012; Acharya & Vijayan, 2015; Chettri, 2015). A declining trend in the species richness of butterflies in the Eastern Himalayan elevational gradient has been documented by Acharya and Vijayan (2015). Nonetheless, the richness trend may show considerable variation in local and regional scale(Rahbek 2005, McCain & Grytnes, 2010). Hence, in order to ensure the generality of the pattern, it is necessary to explore other elevation gradient as well.

Therefore, this study was undertaken to study the pattern of richness and density of butterflies along the elevation gradient of Rangeet Valley, Eastern Himalaya. I also determined the spatial and environmental factors associated with these patterns. I then evaluated the richness and density pattern of different sub-groups (categorized according to their family, elevational range size, biogeographic affinity, and larval host-plant specificity) along the elevation. Lastly, I explored the variation and similarities in the underlying mechanisms of species richness and density gradients between the sub-groups

3.2 Methodology

3.2.1 Butterfly sampling

Pollard walk method (Pollard, 1977) and transect count method (Wood & Gillman, 1998) are often used for sampling butterflies. Since the terrains in the study area are sloppy, Pollard walk or transects counts are not feasible. Hence I used fixed points along the transects to sample butterflies following Acharya and Vijayan (2015). This method has been used in considerable number of previous studies (Chettri et al., 2018; Dewan et al., 2019; Sharma et al., 2020) and is recognized as one of the ideal techniques to sample butterflies (Kral et al., .2018). Butterflies were sampled in different study sites established along an elevation range of 300 m to 3300 m. The total elevational range was categorized into 16 elevation bands with an interval of 150-200 m between each band. In each zone or band, I selected suitable forest sites which were accessible, had good forest cover and had less sign of anthropogenic disturbances. In each site (elevational zone) a transect of 1000m length was established. Within each transects, 10 permanent points spaced 80-100 m apart were established. Butterflies (species and their individuals) within a 5 m radius from the centre of the point were recorded for five minutes. To ensure optimal weather conditions butterflies were sampled only on clear sunny days between 10:00 hrs and 13:00 hrs. Additionally, in order to avoid any time bias with respect to any particular point, butterfly counts were conducted in alternative order along the transect (i.e. starting from 1st point in first sampling but with the last point in the next sampling and so on). Butterflies were identified at wings during sampling using the illustrated guide-books of Haribal (1992) and Kehimkar (2016). Butterflies that remained unidentified were photographed and later identified by referring to guide-books and the ifoundbutterflies website (ifoundbutterflies.org; Kunte et al. 2019). The point count was replicated 3-5 times each covering three major seasons pre-monsoon (March-May), monsoon (June-August), and post-monsoon (September-November)- over the period of two years (2016 to 2018).A total of 1860 point counts spread across 16 transects were completed during the sampling period (**Table 3.1**).

Table 3.1:Observed richness, estimated richness, rarefied richness, number of individuals, and density of butterflies along with effort for each transect along an elevation gradient in Rangeet Valley, Eastern Himalaya.

Study Sites	Elevation midpoint (m)	Effort (point count)	Observed species richness	Chao1	Jack1	Rarefied richness	No of individuals	Density (per ha.)
T1	350	130	121	145.76	155.73	115.03	800	784
T2	500	120	118	173.89	169.57	113.77	497	528
T3	650	120	80	107.2	104.79	77.84	364	386
T4	800	110	69	99.99	95.75	69	291	337
T5	950	120	79	89.56	100.82	77.21	358	380
T6	1150	120	49	64.46	68.83	47.35	179	190
T7	1350	110	58	105.01	85.75	58	201	233
T8	1550	110	36	44.18	47.89	36	123	142
T9	1700	110	56	118.67	84.74	56	189	219
T10	1900	120	31	42.04	43.89	29.87	112	119
T11	2100	120	27	28.65	31.96	26.55	129	137
T12	2300	110	24	26.48	29.95	24	113	131
T13	2500	110	12	12	12.99	12	96	111
T14	2700	120	11	11.99	12.98	10.83	69	73
T15	2900	120	10	10.25	11.98	9.81	54	57
T16	3100	110	8	8	8.88	8	28	32

3.2.2 Species grouping

Butterflies recorded during the study were broadly categorized according to their respective families, range size, biogeographic affinity, and host-plant specialization. According to families, butterflies were grouped as Nymphalidae, Hesperiidae, Lycaenidae, Papilionidae, Pieridae, and Riodinidae. In terms of elevational range size category, butterflies were grouped as having large-range or short-range. Range size categories were assigned by following the method of Wu et al. (2013b). Butterflies with elevational range greater than 1500 m i.e. more than half of the total elevational range covered in the study (3000 m) were considered as large-range and rest as small-range species. Since some species were observed in only one elevation band, 100 m range was assigned to every species (±50 m of the point elevation), assuming the species to be present within this range (Stevens, 1992). Indian butterflies were earlier assigned to have affinity to different biogeographic realms based on the center of their diversity (Holloway, 1974). Following this approach, butterflies were grouped as (a) Global (having a centre of diversity in at least two regions), (b) Oriental (affinity to hot, humid, evergreen forest habitats), and (c) Palearctic (affinity to colder and temperate regions). Few other species had an affinity to the African region while some did not show affinity to any biogeographic realm. Hence, these butterflies were excluded from the group-based analyses of species richness and density trends. In terms of larval host-plant specialization, butterflies were grouped as monophagous (larva feeding on plants in only one genus), oligophagous (larva feeding on plants in a single family, but more than one genus), and polyphagous species (larva feeding on plants in more than one family or order) (Zhang, 2019). Data on host plants were obtained from various secondary sources

(Haribal, 1992; Kehimkar, 2008) supplemented by field observations. Information on host pant of 72 species was missing while larvae of two species were carnivores, hence, analysis of trend of these species were not possible.

3.2.3 Spatial variables

Area

For the calculation of area of each elevational band, Digital Elevation Model (DEM) imagery (covering the Sikkim Himalayan region) generated from the Cartosat-1 satellite was downloaded (built and operated by the Indian Space Research Organization (ISRO). Cartosat-1 DEMs is freely available on Bhuvan, an online Indian geospatial platform (http://bhuvan.nrsc.gov.in). The DEM image contains elevation data in each raster cell. The DEM raster was first classified into series of elevational zones (150-200m bands) using the spatial analyst toolbox in ArcGIS 10.4. I then calculated the area of each reclassified elevation band using the zonal geometry tool in ArcGIS 10.4.

3.2.4 Environmental variables

Vegetation

Trees and shrubs were sampled along the same transects that were established for sampling butterflies. For trees, quadrats of 10x10 m size were established adjacent to the butterfly sampling points. Plants with DBH (diameter at breast height) ≥20 cm were considered as trees. Sub-quadrats (5x5 m) were laid diagonally within each 10x10 m quadrat for sampling shrubs. In the quadrats, species richness and density of trees and shrubs were estimated. Altogether 10 quadrats for trees and 20 quadrats for shrubs were laid at each elevational zone.

Normalized Difference Vegetation Index (NDVI) was used as a surrogate for above-ground productivity (Nieto et al., 2015). Three years (2016-2018) of Landsat8 imagery data (available at 30 m resolution) of the Sikkim Himalayan region, was acquired from the USGS website (http://earthexplorer.usgs.gov) for the estimation of NDVI. The Landstat8 consists of 11 spectral bands out of which red and near-infrared were used for calculating NDVI. The three years of individual red and near-infrared rasters was averaged into a single raster dataset using ArcGIS 10.4. NDVI was then calculated from these averaged outputs using the formula-

NDVI = (Near Infrared – Red) / (Near Infrared + Red)

in ArcGis10.4. The final output consists of NDVI values in each pixel. I averaged the NDVI values of a central pixel plus eight adjacent pixels in the raster. The central pixels corresponds to the midpoint of transects established for sampling butterflies. Taking the NDVI from nine pixels ensures that information from all points along the transects are taken into account.

Climatic variables

High resolution, interpolated climatic datasets prepared by CHELSA (Climatologies at high resolution for the Earth’s land surface areas) (Karger et al. 2017a, b) were used in the study. There are 19 bio-climatic variables available in the datasets but only mean annual precipitation (MAP) and mean annual temperature (MAT) was considered as these variables directly affect the distribution of butterfly biodiversity. Besides, other bio-climatic variables are mostly derived from these two variables. The CHELSA dataset has a resolution of 30 arc seconds (1 km^2 grid) and is available in a raster format. Since the raw raster image consists of the information of the entire globe, I first clipped the image into the area that corresponds to geographic boundary of Sikkim. Values of MAT and MAP for consecutive elevation bands were obtained by averaging the grid values falling within each band using ArcGIS 10.4. Using the MAT and MAP data, annual actual evapotranspiration (AET) was calculated using Turc's formula (1954)-

$AET = P/ [0.9 + (P/ L) 2]1/2$,

where $L = 300 + 25T + 0.05T3$,

P = mean annual precipitation and,

T = mean annual temperature.

AET is a function of water availability and temperature and, hence, has been used as a measure of water-energy balance (Hawkins & Porter, 2003a). Potential evapotranspiration was estimated following Holdridge et al. (1971)-

PET = mean annual bio-temperature (i.e. temperature >0^{O} C) x 58.93]

PET is considered as a measure of ambient energy (Hawkins & Porter, 2003a).

3.2.5 Data analysis

Observed species richness was considered as a total number of species recorded in all seasons within elevational band during the study period. Observed species richness may not always be a reliable estimate of richness since it is practically impossible to detect all species present during sampling. Hence, non-parametric estimators of richness and rarefied richness were also used (Colwell & Elsensohn, 2014). Among list of richness estimators, Chao1 and Jackknife1 estimators were selected owing to their high precision in estimating richness (Hortal et al., 2006). For rarefaction species richness was rarified to the lowest number of counts conducted for any site (110 point counts). To compare observed species richness with the estimated richness and to assess the completeness of the sampling, species accumulation curves were generated using point count as an effort. Of all the species richness measures Jackknife1 predicted a higher number of species in most of the sites. Hence, only Jackknife1 was used as the measure of species richness for all the butterfly groups.

I also recorded abundance (total number of individuals) of butterflies in each elevation band. In order to account for variability in number of individuals encountered due to unequal sampling, abundance data was converted into density. Density was considered as total number of individual butterflies recorded per unit area irrespective of the species richness. Density was estimated following the approach used for birds (Reynolds et al., 1980)-

$D = n * 10000 / \pi r^2 C$,

where D = butterfly density (numbers ha^{-1}), n = total number of butterflies observed in all counts within the specific radius, r (m) (specific radius is the average radial distance of butterflies from the observer), and C = total number of counts conducted. From the overall pooled data,density of all the sub-groups of butterflies in each elevational band was estimated.

In order to assess the relationship between elevation and observed species richness, estimated richness, rarefied species richness, total density, and species richness and density of the sub-groups, scatter plots were drawn using the *ggplot2* package (Wickham, 2016) in R software (version 3.4.3). Since richness estimates and density of most sub-groups showed a linear trend with elevation,I used ordinary least squares regression to test the significance of the relationship. In order to explore the relationship between species richness and density of butterflies with different predictor variables generalized linear modeling (GLM) with a log link function assuming a Poisson distribution of error function was used. Prior to GLM analysis predictor variables were subjected to multicollinearity test. Since MAT ($r = 0.998$, $p < 0.01$), MAP ($r = -0.874$, $p < 0.01$), and PET ($r = 1$, $p < 0.01$) were removed from the GLM modeling because they showed high correlation to AET. In the final set of parameters, species richness and density was taken as dependent variables while AET, tree species richness, tree density, shrub species richness, shrub density, NDVI and area were taken as predictor variables. Using these parameters, total of 128 GLMs were generated using the package *glmulti* (Calcagno & de Mazancourt, 2010) in R software (version 3.6.3). The best fitting GLM is considered as the one that has the lowest corrected Akaike information criterion (AIC_c) value than rest of the other model sets. Models with a $\Delta AIC_c < 2$ from the model with the lowest AIC_c are

are also considered equally likely (Burnham & Anderson, 2002). Hence, average of all likely models were used to estimate the relative importance of each of the predictor variables in the models (Johnson& Omland, 2004). The model averaging was conducted using the package *MuMin* (Barton & Barton, 2013)in R software (version 3.6.3).

3.3 Results

3.3.1 Species richness and density of butterflies along the elevational gradient

A total of 3603 individual butterflies representing 253 species and six families were recorded during the study (**Table 3.1; Table A 3.1; Photo plate 3.1-3.6**). In terms of species richness Nymphalidae was the most dominant family with 117 species followed by Lycaenidae with 42 species, Hesperiidae with 39 species, Pieridae with 25 species, Papilionidae with 24 species, and Riodinidae with six species(**Figure 3.1**). Out of all butterfly species recorded, 22 species had a large range size while the other 231 species had a small range. In terms of the biogeographic affinity, 23 species belonged to the global category, 208 were Oriental, and 10 were Palearctic. Out of total butterflies, 43 species were monophagous, 75 species oligophagous, and 61 species polyphagous in nature. Out of the total individuals of butterflies recorded during the study, 51.65% belonged to Nymphalidae (1861 individuals), 18.20% to Pieridae (656), 12.10%to Papilionidae (436), 9.99% to Lycaenidaes (360), 4.635% to Hesperiidae (167) and 3.41% to Riodinidae (123) (**Figure 3.1**). A total of 25.84% of butterflies (930) had large range while 74.15% (2668) had small range size. In terms of biogeographic affinity, 18.27% (634) butterflies belonged to Global, 76.88% (2667) belonged to Oriental and 4.84% (168) belonged to Palearctic category. Regarding host plant specialization, 24.45% (776)

butterflies were Monophagous, 50% (1584) Oligophagous and 25.50% (808) Polyphagous individuals.

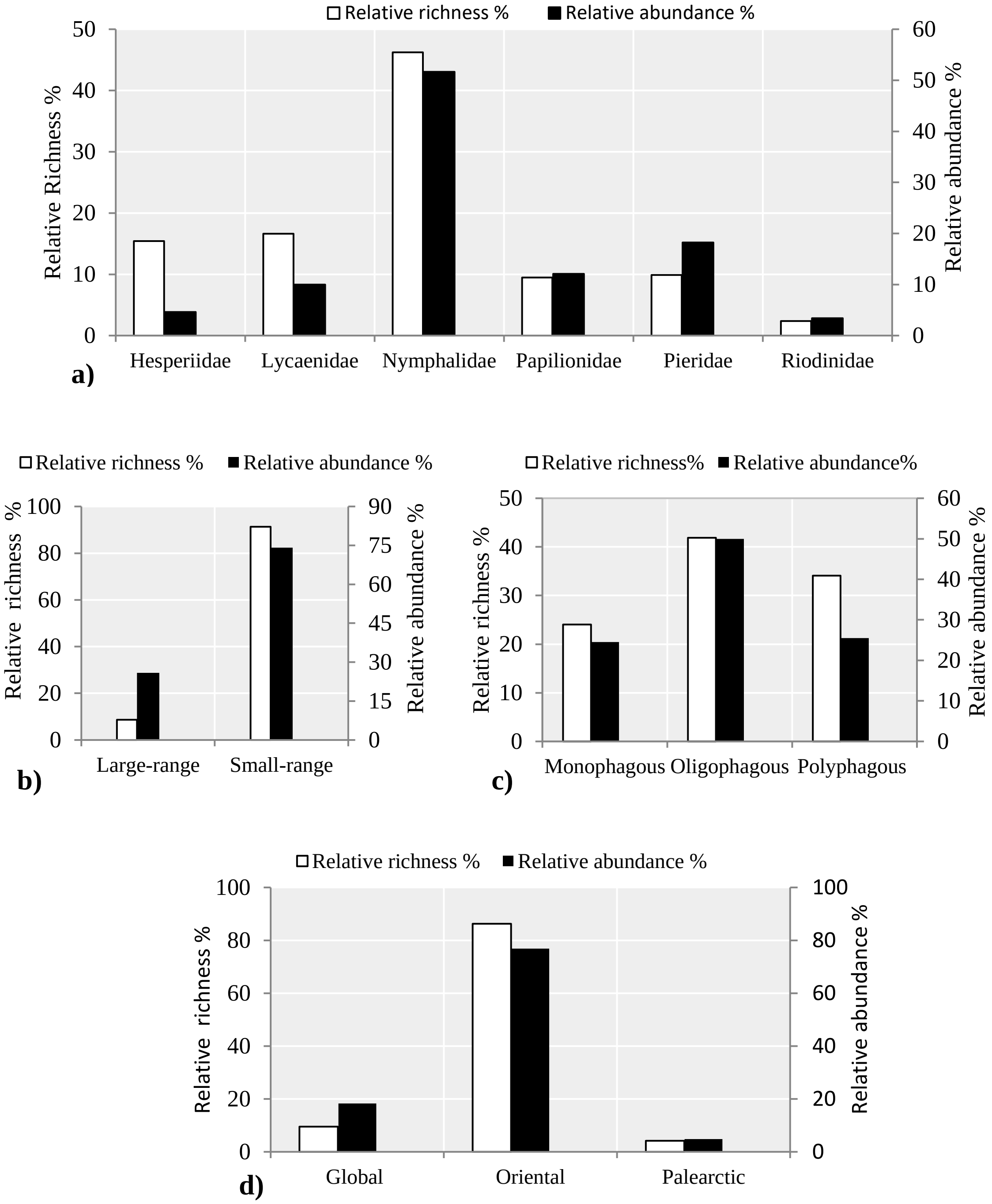


Figure 3.1: Relative richness and abundance of different sub-groups of butterflies in the Rangeet Valley; a) Family, b) Range-Size c) Larval-host specificity d) Biogeographic affinity.

Among the different richness estimators, Jackknife1 predicted a slightly higher number of species, for each elevation band, indicating more species could be counted with further sampling. However, species accumulation curve predicted that the rate of addition of species would be uniformly low indicating that the sampling effort was almost complete for the present study (**Figure 3.2**).

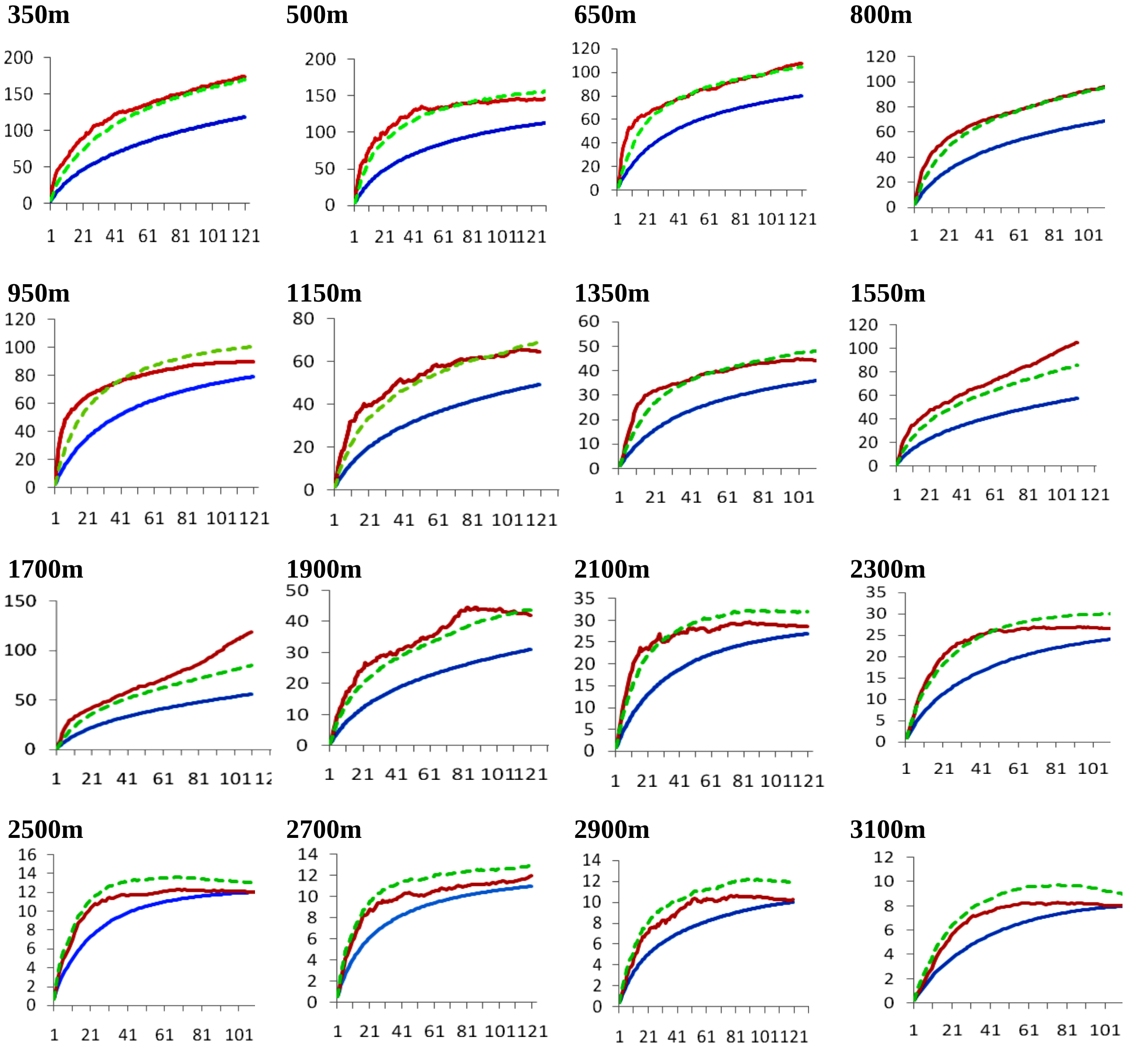


Figure 3.2: Species accumulation curves of butterflies observed at different elevations (in m above sea level) in Rangeet Valley, Sikkim, Eastern Himalaya. The blue line repsesents observed richness, the red represents Chao1 and green dotted line denotes Jackknife 1 estimates. x axis= Total number of point counts, y axis= Species richness.

The observed species richness of butterflies followed a declining trend with increase in elevation (**Table 3.2**; **Figure 3.3**). Estimated richness (Jackknife1) also followed a declining trend with a slight hump at around 500 m elevation ($R^2 = 0.868$, $p < 0.01$). Similarly, declining trend with increasing elevation was also observed in case of rarefied species richness ($R^2 = 0.883$, $p < 0.01$). The species richness of butterfly families such as Nymphalidae ($R^2 = 806$, $p < 0.01$), Papilionidae ($R^2 = 0.806$, $p < 0.01$), Hesperiidae ($R^2 = 0.684$, $p < 0.01$), Lycaenidae ($R^2 = 0.890$, $p < 0.01$) and Pieridae ($R^2 = 0.768$, $p < 0.01$) followed but declining trend with elevation but family Riodinidae did not show any definite trend. The species richness of the small-range butterflies followed a distinct linear decline with elevation ($R^2 = 0.836$, $p < 0.01$), whereas the large-range species had two distinct peaks (one at 500 m and other at 1700m) and fitted poorly to the linear regression models. Species richness pattern of Global ($R^2 = 0.844$, $p < 0.01$) and Oriental ($R^2 = 0.836$, $p < 0.01$) species declined linearly with an increase in elevation but not trends were observed in case of Palearctic species. Similarly, butterflies belonging to all three polyphagy groups i.e oligophagous ($R^2 = 0.909$, $p < 0.01$), monophagous ($R^2 = 0.583$, $p < 0.01$) and polyphagous ($R^2 = 0.786$, $p < 0.01$) declined with elevation.

The total density of butterflies ($R^2 = 0.740$, $p < 0.01$) showed a linear decline with increasing elevation (**Table 3.3; Figure. 3.4**). Similarly, density of Nymphalidae ($R^2 = 0.370$, $p < 0.05$), Papilionidae, ($R^2 = 0.530$, $p < 0.01$), Hesperiidae ($R^2 = 0.520$, $p < 0.01$), Pieridae ($R^2 = 0.250$, $p < 0.01$) and Lycaenidae ($R^2 = 0.370$, $p < 0.05$) families as well as small-range ($R^2 = 0.320$, $p < 0.05$), Global ($R^2 = 0.740$, $p < 0.01$), oligophagous ($R^2 = 0.330$, $p < 0.05$), and polyphagous ($R^2 = 0.320$, $p < 0.05$) butterflies showed a declining trend along the elevation gradient.

Table 3.2: Ordinary least squares regression of observed (overall), estimated and rarefied species richness as well as sub-groups of butterflies with elevation in Sikkim, Eastern Himalaya.

Species richness	**Coefficient**	**Std. Error**	**R^2**	**t-value**	**Pr(>|t|)**
Observed	-0.039	0.004	0.876	-9.941	**<0.001****
Chao1	-0.053	0.007	0.794	-7.334	**<0.001****
Jackknife1	-0.053	0.006	0.868	-9.586	**<0.001****
Rarefied	-0.037	0.004	0.883	-10.280	**<0.001****
Nymphalidae	-0.022	0.002	0.806	-7.628	**<0.001****
Papilionidae	-0.007	0.001	0.833	-8.378	**<0.001****
Hesperiidae	-0.009	0.001	0.684	-5.515	**<0.001****
Lycaenidae	<-0.001	0.001	0.898	-2.872	**<0.001****
Riodinidae	< -0.001	0.000	0.001	-0.133	0.980
Pieridae	-0.006	0.001	0.768	-6.817	**<0.001****
Large-range	-0.005	0.001	0.649	-5.098	**0.001****
Small-range	-0.047	0.005	0.836	-8.471	**<0.001****
Global	-0.007	0.001	0.844	-8.471	**<0.001****
Palearctic	<-0.001	0.000	0.050	-0.862	0.403
Oriental	-0.041	0.004	0.847	-8.821	**<0.001****
Monophagous	-0.008	0.001	0.534	-4.009	**0.001****
Oligophagous	-0.018	0.001	0.909	-11.880	**<0.001****
Polyphagous	-0.017	0.002	0.786	-7.188	**<0.001****

Coefficient of regression, standard error (Std. Error), R^2 representing the proportion of variance of regression, and t-value along with overall significance of the regression are presented. ** Significant at $p < 0.01$, Negative relationships are indicated by minus (-) sign. Significant p-values are highlighted as bold font

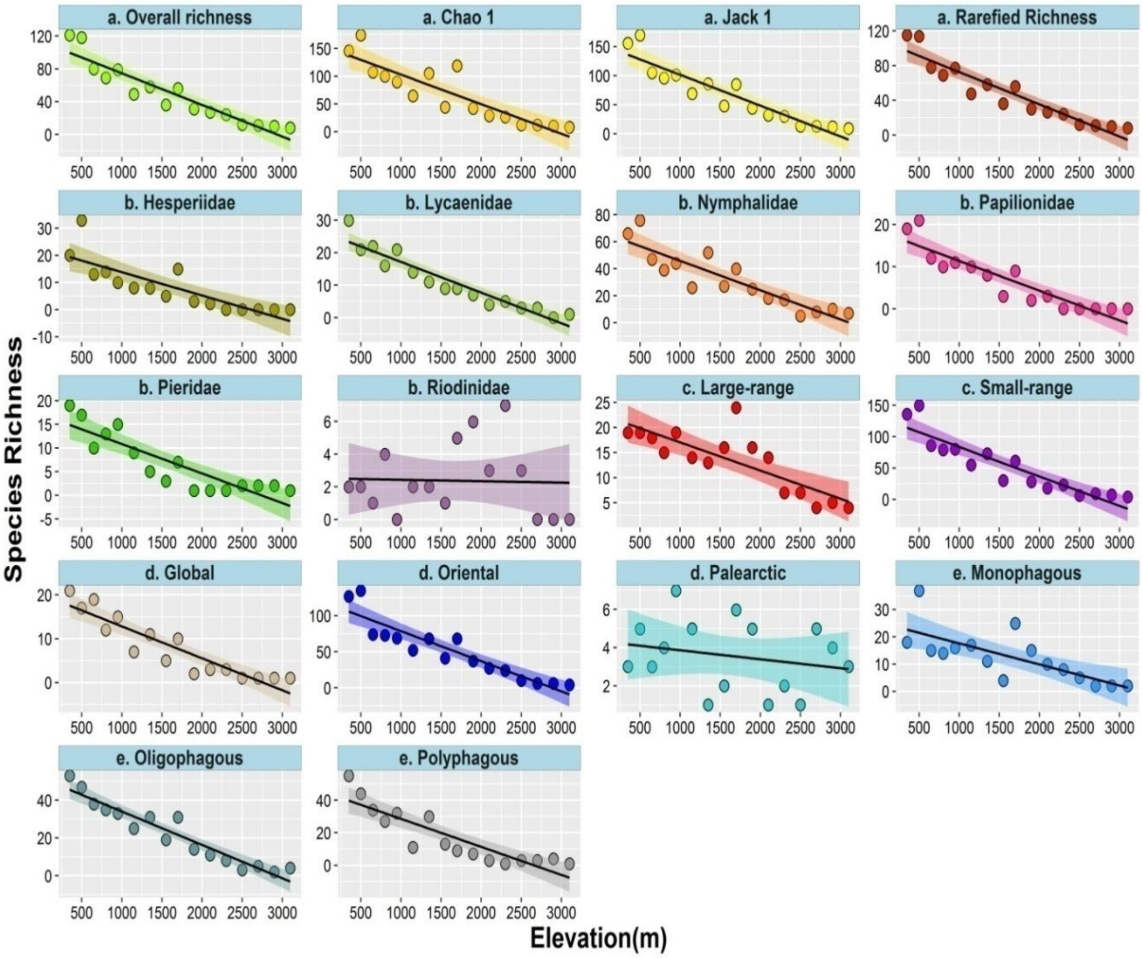


Figure 3.3: Scatter plots of butterfly species richness and elevation in the Eastern Himalaya; a) Overall, estimated (Chao 1 and Jackknife 1), and rarefied species richness, b) by family, c) range size, d) geographic affinity, and e) feeding guild. A linear trend line with shading representing the 95% confidence interval has been fitted to each plot. The linear trend observed in overall richness, Chao1, Jackknife1, rarefied richness and richness of Hesperiidae Lycaenidae, Nymphalidae, Papilionidae, Pieirdae, Large-range, Small-Range, Global, Oriental, monophagous, oligophagous and polyphagous are statistically significant ($p<0.01$). Richness trend of Riodinidae and Palearctic species are non-significant.

Table 3.3: Ordinary least squares regression of density (total and sub-groups) of butterflies with elevation in Sikkim, Eastern Himalaya.

Density (per h.a)	**Coefficient**	**Std. Error**	**R^2**	**t-value**	**Pr(>|t|)**
Total Density	-0.190	0.030	0.740	-6.390	**<0.001****
Nymphalidae	-0.060	0.020	0.370	-2.850	**0.013 ***
Papilionidae	-0.020	-0.020	0.530	-3.940	**0.002 ****
Hesperiidae	-0.010	0.000	0.520	-3.900	**0.001 ****
Lycaenidae	-0.010	0.000	0.370	-2.890	**0.012 ***
Riodinidae	0.000	0.000	0.020	0.550	0.590
Pieridae	-0.030	0.010	0.250	-2.150	**0.051 ***
Large-range	-0.010	0.010	0.070	-1.040	0.310
Small-range	-0.100	0.040	0.320	-2.570	**0.022 ***
Global	-0.030	0.010	0.400	-3.070	**0.008 ****
Palearctic	0.400	0.000	0.700	0.400	0.700
Oriental	0.000	0.000	0.190	-1.820	0.090
Monophagous	-0.020	0.010	0.160	-1.640	0.120
Oligophagous	-0.080	0.030	0.300	-2.460	**0.027 ***
Polyphagous	-0.050	0.020	0.320	-2.560	**0.022 ***

Coefficient of regression, standard error (Std. Error), R^2 representing the proportion of variance of regression, and t-value along with overall significance of the regression are presented. *Significant at $p < 0.05$, ** significant at $p < 0.01$. Negative relationships are indicated by a minus (-) sign. Significant p-values are highlighted as bold font.

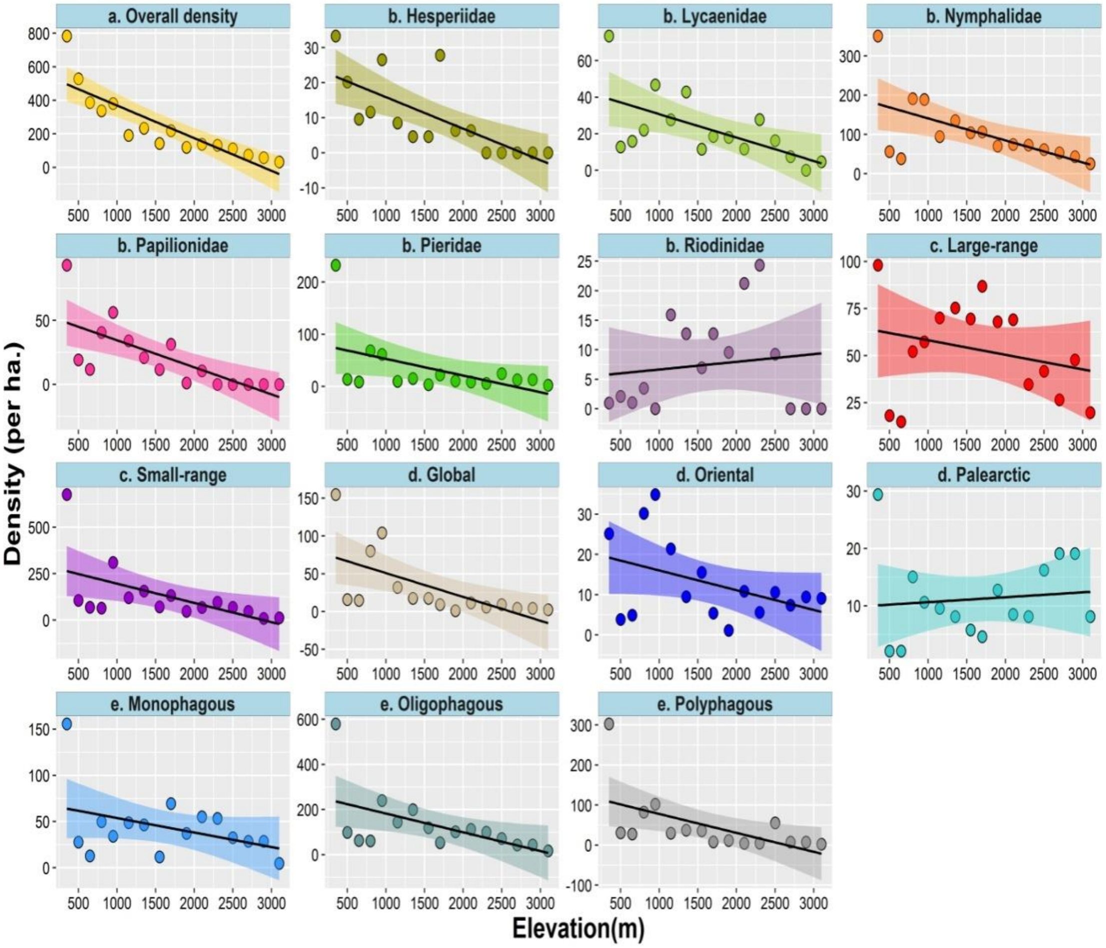


Figure 3.4: Scatter plots of butterfly density and elevation in the Eastern Himalaya; a) Overall, b) by family, c) range size, d) geographic affinity, and e) feeding guild. A linear trend line with shading representing the 95% confidence interval has been fitted to each plot. The linear trend observed in overall density and density of Papilionidae, Hesperridae and Global butterflies are significant at $p<0.01$. Density pattern of Nymphalidae, Lycaenidae, Pieridae, Small-range, oligophgaous and polyphagous butterflies are significant at $p<0.05$. Density trend of Riodinidae, Large-range, Palearctic, Oriental and monophagous butterflies are not significant.

3.3.2 Determinants of butterfly species richness and density

Out of the 128 generalized linear models generated, two candidate model sets had the lowest AIC_c and therefore was the best explanation for variation in overall species richness pattern of butterflies along the elevation gradient (**Table 3.4**). Inference generated by averaging all the best likelihood models suggests AET followed by tree density as the best explanatory variables causing variation in overall species richness of butterflies along the elevation (**Table 3.5**). Similarly, variation in species richness of different sub-groups of butterflies was explained by different sets of models. AET significantly influenced the species richness pattern of most sub-groups of butterflies except for Riodinidae, large-range and Palearctic species. Variables such as tree species richness were found to strongly affect species richness pattern of Hesperiidae and Monophagous butterflies. Similarly, tree density was an important determinant of overall butterfly species richness as well as richness of Nymphalidae and oligophagous butterflies. Species richness of Riodinidae family, large-range and Palearctic butterflies did not show any significant relationship with any spatial or environmental variables. The generalized linear models suggest that AET followed by shrub density was the most significant predictor of total butterfly density along the elevation gradient (**Table 3.6, 3.7**). Among the different sub-groups of butterflies, AET had significant effect on density of family Lycaenidae only. Habitat variables such as shrub density significantly affected the density of Pieridae, small-range, oligophagous and polyphagous butterflies. Similarly, tree density significantly affected density of Hesperiidae butterflies. Species richness of shrubs was, however, found to have negative influence on the density of certain sub-groups of butterflies such as Papilionidae, Pieridae and Palearctic species.

Table 3.4: Best candidate generalized linear models describing the relationship between species richness of butterflies and selected predictor variables along an elevation gradient in the Eastern Himalaya. Models with a $\Delta AIC_c < 2$ from the top model set are included.

	Models	**k**	**AIC$_c$**	***Δi***	***wi***
Overall species richness	~ 1 + TSR + TRD + AET + SSD	6	133.312	0	0.336
	~ 1 + TSR + TRD + AET	5	133.512	0.2	0.303
Nymphalidae	~ 1 + TSR + TRD + AET	5	115.041	0	0.330
	~ 1 + TRD + AET	4	116.631	1.59	0.149
Papilionidae	~ 1 + TSR + AET	4	66.863	0	0.159
	~1 + AET + Area	4	67.524	0.661	0.145
	~1 + TSR + AET + Area	5	67.792	0.929	0.100
	~1 + TSR + NDVI + AET	5	68.537	1.674	0.068
Pieridae	~ 1 + SSR + AET	4	67.456	0	0.309
	~ 1 + AET	3	69.368	1.912	0.107
Lycaenidae	~ 1 + AET	3	75.264	0	0.254
	~ 1 + AET + Area	4	77.126	1.862	0.100
Hesperiidae	~ 1 + TSR + AET	3	70.738	0	0.263
	~ 1 + TSR + TRD + AET	5	71.138	0.4	0.215
Riodinidae	~ 1 + TRS	2	70.595	0	0.079
	~ 1 + TRD	3	71.077	0.482	0.058
	~1+TSR + Area	4	71.287	0.692	0.052
	~ 1	2	71.398	0.803	0.049
	~ 1 + TRD + Area	4	71.431	0.836	0.048
	~ 1 + Area	3	71.531	0.936	0.046
	~ 1 + TSR + AET	4	71.706	1.111	0.042
	~1 + TRD + SSD	4	71.982	1.387	0.037
	~ 1 + TRD + NDVI	4	72.308	1.713	0.031
	~ 1 + TSR + NDVI	4	72.441	1.846	0.029
Large-range	~ 1 + TSR + TRD + AET	4	87.909	0	0.153

	~ 1 + TRD + AET + Area	4	89.001	1.092	0.088
	~ 1 +TRD + AET	4	89.192	1.283	0.080
	~1 + TSR + TRD	4	89.259	1.35	0.077
	~ 1 + TRD + AET + SSD	5	89.552	1.643	0.067
	~ 1 + TSR + AET	4	89.601	1.692	0.065
Small-range	~ 1 + TSR + TRD +AET + SSD	6	134.871	0	0.286
	~ 1 + TSR + TRD + AET	5	136.255	1.384	0.143
	~ 1 + TRD + AET + SSD	5	136.657	1.786	0.171
Global	~ 1 + AET	3	72.118	0	0.265
	~ 1 + AET + Area	4	73.930	1.812	0.107
Oriental	~ 1 + TSR + TRD + AET	5	122.455	0	0.540
Palearctic	~ 1+ SSR	3	64.965	0	0.111
	~ 1 + NDVI	3	65.7960	0.831	0.073
	~ 1	2	66.197	1.232	0.060
	~ 1 + SSR + NDVI		66.226	1.261	0.059
	~ 1 + SSR + AET		66.345	1.38	0.056
Monophagous	~ 1 + TSR + SSR + AET	5	101.266	0	0.278
	~ 1 + TSR + AET	4	101.962	0.696	0.189
Oligophagous	~ 1 + TRD + AET + Area	5	96.198	0	0.231
	~ 1 + TSR + AET + SSD	5	97.898	1.7	0.098
	~ 1 + AET + Area	4	98.040	1.842	0.092
Polyphagous	~ 1 + AET	3	96.471	0	0.145
	~ 1 + AET + TRD	4	96.513	0.042	0.142
	~ 1 + TRD + AET + SSD	5	97.510	1.039	0.086
	~ 1 + AET + Area	4	97.651	1.18	0.080
	~ 1 + TRD + AET + Area	5	97.951	1.48	0.069

k = number of parameters in the model; Δi= AIC$_c$of best fitting model and that of model *i*;*wi*= weight of evidence that model *i* is the best approximating model. AET (Actual Evapotranspiration);TSR (Tree Species Richness); TRD (Tree Density); SSR (Shrub Species Richness);SSD (Shrub Density);NDVI (Normalized Difference Vegetation Index).

Table 3.5: Summary of model averaged estimates (generalized linear model) of predictor variables in explaining variation in species richness of butterflies along the elevation gradient in Sikkim, Eastern Himalaya using multimodal inference.

	Variables	**Estimate**	**Std.Er**	**Z-value**	**P-value**
Overall Richness	AET	0.004	0.001	9.246	**<0.001****
	TRS	0.024	0.007	2.812	**0.005 ****
	TRD	0.002	0.001	2.822	**0.004 ****
	SSD	-0.001	0.001	0.838	0.402
Nymphalidae	AET	0.003	0	8.261	**<0.001****
	TRS	0.03	0.269	2.947	**0.003****
	TRD	0.002	0.001	1.112	0.261
Papilionidae	AET	0.007	0.002	2.975	**0.002****
	TRS	0.056	0.026	1.935	0.53
	NDVI	-5.727	4.155	1.24	0.215
	Area	0.004	0.002	1.73	0.083
Pieridae	AET	0.004	0.001	7.09	**<0.001****
	SSR	-0.037	0.01	1.989	**0.046***
Hesperiidae	AET	0.005	0.001	6.804	**<0.001****
	TSR	0.094	0.021	4.065	**<0.001****
	TRD	0.002	0.003	0.692	0.489
Lycaenidae	AET	0.004	0.001	5.988	**<0.001****
	Area	0.001	0.001	0.406	0.685
Riodinidae	AET	-0.0001	0.001	0.242	0.809
	TSR	0.021	0.03	0.67	0.503
	TRD	0.002	0.003	0.614	0.539
	SSD	-0.001	0.001	0.224	0.823
	NDVI	0.609	2.079	0.281	0.779
	Area	0.001	0.002	0.508	0.612
Large-range	AET	0.001	0.001	1.437	0.15

	TSR	0.019	0.02	0.932	0.351
	TRD	0.003	0.002	1.699	0.089
	SSD	-0.001	0.001	0.316	0.751
	Area	0.001	0.001	0.377	0.706
Small-range	AET	0.005	0.001	14.547	**<0.001****
	TSR	0.0182	0.012	1.411	0.158
	TRD	0.002	0.001	2.325	**0.020 ***
	SSD	-0.001	0.001	1.277	0.201
Global	AET	0.004	0.001	5.225	**<0.001****
	Area	0.001	0.001	0.414	0.679
Oriental	AET	0.004	0.001	14.157	**<0.001****
	TSR	0.039	0.007	5.265	**<0.001****
	TRD	0.0029	0.001	3.636	**<0.001****
Palearctic	SSR	-0.028	0.029	0.922	0.356
	NDVI	-1.922	3.395	0.56	0.575
	SSD	0.001	0.001	0.315	0.752
Monophagous	AET	0.002	0.001	3.9	**<0.001****
	TSR	0.065	0.014	4.025	**<0.001****
	SSR	-0.014	0.014	0.907	0.364
Oligophagous	AET	0.005	0.001	6.903	**<0.001****
	TRD	0.002	0.001	2.099	0.255
	SSD	-0.001	0	0.653	0.923
	Area	0.003	0.001	2.611	**0.02 ***
Polyphagous	AET	0.005	0.001	6.915	**<0.001****
	TRD	0.001	0.001	0.846	0.400
	SSD	-0.001	0.001	0.355	0.722
	Area	0.001	0.001	0.464	0.642

Parameter estimate, standard deviation of the parameter estimates, z-score and significance of each predictor variable are provided. Significant variables are marked in bold. *Significant at p <0.05, ** significantat p <0.01. AET (Actual Evapotranspiration); TSR (Tree Species Richness); TRD (Tree Density); SSR (Shrub Species Richness); SSD (Shrub Density); NDVI (Normalized Difference in Vegetation Index).

Table 3.6: Best candidate generalized linear models describing the relationship between density of butterflies and selected predictor variables along an elevation gradient in the Eastern Himalaya. Models with a $\Delta AIC_c < 2$ from the top model set are included.

	Models	**k**	**AIC$_c$**	***Δi***	***wi***
Total Density	~ 1 + AET + SSD	4	187.948	0.000	0.284
	~ 1 + SSR + AET + SD	5	188.045	0.097	2.701
Nymphalidae	~ 1 + AET	3	186.103	0.000	0.084
	~ 1 + TRD + SSD	4	186.255	0.153	0.078
	~ 1 + TRD + Area	4	186.594	0.491	0.066
	~ 1 + TRD	3	186.860	0.757	0.058
	~ 1 + SSR + AET	4	186.876	0.774	0.057
	~ 1 + SSD	3	186.942	0.839	0.055
	~ 1 + TRD + AET	4	186.962	0.860	0.055
	~ 1 + TRD + SSR + AET	5	187.845	1.742	0.035
	~ 1 + AET + SSD	4	188.001	1.898	0.033
Pieridae	~ 1 + SSR + SSD	4	165.605	0.000	0.279
	~ 1 + TRD + SSR + SSD	5	167.372	1.767	1.155
Riodinidae	~ 1 + Area	3	112.543	0.000	0.143
	~ 1 + TSR + Area	4	112.659	0.115	0.135
	~ 1 + AET + Area	4	114.508	1.964	0.053
Hesperiidae	~ 1 + TRD + SSR + AET	5	113.777	0.000	0.221
	~ 1 + TRD + Area	4	114.507	0.730	0.153
Lycaenidae	~ 1 + AET	3	138.593	0.000	0.205
	~ 1 + TSR + AET	4	139.457	0.864	0.063
Papilionidae	~ 1 + SSR + AET	4	141.139	0.000	0.312
	~ 1 + TRD + SSR + AET	5	143.116	1.978	0.114
Large-range	~ 1 + SSR + AET + SSD + Area	7	146.569	0.000	0.295
	~ 1 + TRD	3	148.557	1.988	0.109
Small-range	~ 1 + SSD	3	205.048	0.000	0.232
	~ 1 + TRD + SSD	4	206.894	1.845	0.092

Global	~ 1 + SSR + AET	4	163.183	0.000	0.103
	l ~ 1 + SSR + AET + SSD	5	163.808	0.625	0.076
	~ 1 + TRD + Area	4	163.902	0.719	0.072
	~ 1 + SSD	3	164.670	1.487	0.049
	~ 1 + Area	3	164.850	1.667	0.045
	~ 1 + AET	3	164.906	1.722	0.044
Oriental	~ 1 + AET	3	122.288	0.000	0.120
	~ 1 + SSR + AET	4	122.500	0.213	0.108
	~ 1	2	122.787	0.499	0.094
	~ 1 + Area	3	123.769	1.481	0.057
	~ 1 + NDVI	3	124.170	1.883	0.047
Palearctic	~ 1 + SSR + SSD + Area	5	108.995	0.000	0.158
	~ 1 + SSR + SSD	4	109.365	0.370	0.131
	~ 1 + SSR	3	109.857	0.862	0.103
Monophagous	~ 1 + SSD	3	160.887	0.000	0.126
	~ 1 + SSR + SSD	4	162.149	1.262	0.067
	~ 1	2	162.755	1.869	0.049
Oligophagous	~ 1 + SSD	3	200.086	0.000	0.243
	~ 1 + TRD + SSD	4	201.900	1.814	0.087
Polyphagous	~ 1 + SSD	3	175.328	0.000	0.257
	~ 1 + SSR + SSD	4	176.386	1.058	0.152

k = number of parameters in the model; Δi = AIC$_c$of best fitting model and that of model *i*;*wi*= weight of evidence that model *i* is the best approximating model. AET (Actual Evapotranspiration);TSR (Tree Species Richness); TRD (Tree Density); SSR (Shrub Species Richness); SSD (Shrub Density);NDVI (Normalized Difference in Vegetation Index).

Table 3.7: Summary of model averaged estimates (generalized linear model) of predictor variables in explaining variation in butterfly density (numbers per h.a) along the elevation gradient in Sikkim, Eastern Himalaya using multimodal inference.

	Variables	**Estimate**	**Std.Er**	**Z-value**	**P-value**
Total Density	AET	0.587	0.107	5.000	**<0.001****
	SSR	-2.254	2.859	0.758	0.449
	SSD	0.527	0.116	4.122	**<0.001****
Nymphalidae	AET	0.111	0.131	0.828	0.408
	TRD	0.386	0.429	0.870	0.384
	SSR	-0.724	1.881	0.372	0.71
	SSD	0.065	0.114	0.558	0.577
	Area	-0.049	0.147	0.323	0.747
Papilionidae	AET	0.112	0.081	1.238	0.216
	TRD	0.112	0.081	1.238	0.215
	SSR	-1.602	0.592	2.434	**0.014 ***
Pieridae	TRD	0.006	0.004	1.323	0.186
	SSR	-0.184	0.067	2.471	**0.013 ***
	SSD	0.003	0.001	6.337	**<0.001****
Hesperiidae	AET	0.019	0.017	0.1.077	2813
	TRD	0.102	0.037	2.554	**0.011 ***
	SSR	-0.351	0.344	0.988	0.323
	Area	-0.026	0.034	0.752	0.452
Lycaenidae	AET	0.059	0.022	0.2.462	**0138 ***
	TSR	-0.175	0.469	0.354	0.723
Riodinidae	AET	0.002	0.007	0.309	0.757
	TSR	0.168	0.251	0.647	0.518
	Area	0.061	0.024	2.360	**0.019 ***
Large-range	AET	0.086	0.058	1.469	0.142
	TRD	0.076	0.136	0.555	0.579
	SSD	0.112	0.077	1.412	0.158

	SSR	-1.602	1.126	1.379	0.168
	Area	0.425	0.274	1.530	0.126
Small-range	TRD	0.214	0.469	0.435	0.663
	SSD	0.590	0.181	2.990	**0.003****
Global	AET	0.080	0.078	0.999	0.318
	TRD	0.057	0.136	0.411	0.681
	SSR	-1.252	1.576	0.772	0.44
	SSD	0.038	0.065	0.572	0.567
	Area	-0.100	0.162	0.606	0.545
Oriental	AET	0.013	0.015	0.847	0.397
	SSR	-0.153	0.314	0.637	0.472
	NDVI	-7.860	29.305	0.258	0.797
	Area	-0.006	0.018	0.302	0.763
Palearctic	SSR	-0.680	0.239	2.604	**0.009 ****
	SSD	0.030	0.018	1.609	0.10
	Area	0.067	0.033	1.828	0.06
Monophagous	SSR	-0.460	0.961	0.460	0.646
	SSD	0.080	0.056	1.364	0.173
	TRD	0.160	0.379	0.402	0.68
	SSD	0.468	0.154	2.772	**<0.001****
Polyphagous	SSR	-2.716	1.801	1.368	0.171
	SSD	0.322	0.068	4.313	**<0.001****

Parameter estimate, standard deviation of the parameter estimates, z-score and significance of each predictor variables are provided. Significant variables are marked in bold . *Significant at p <0.05, **significant at p <0.01. AET (Actual Evapotranspiration); TSR (Tree Species Richness); TRD (Tree Density); SSR (Shrub Species Richness); SSD (Shrub Density); NDVI (Normalized Difference in Vegetation Index).

3.4 Discussion

3.4.1 Species richness and density along the elevation gradient

The study examined the species richness pattern of butterfly community along the elevation gradient in Rangeet Valley, Sikkim, Eastern Himalaya. A total of 253 species of butterflies were recorded in the study that represents about 36.71% of total butterflies reported from the Sikkim Himalayan region (Haribal, 1992). Species richness and density of butterflies declined monotonically with an increase in elevation in the Rangeet Valley. In the Himalaya, mid elevation peak has been demonstrated in some groups such as plants (Oommen & Shanker, 2005; Acharya et al., 2011b, Sharma et al., 2019), amphibians (Fu et al., 2006; Chettri & Acharya, 2020), birds (Acharya et al., 2011a; Wu et al., 2013a) and mammals (Wu et al., 2013b; Hu et al., 2017). However, monotonic decline in species richness of butterflies has been frequently reported from the Himalaya and elsewhere (Sánchez-Rodríguez &Baz, 1995; Kumar et al., 2009; Bhardwaj et al., 2012; Leingärtner et al., 2014; Acharya & Vijayan, 2015; Chettri, 2015). Hence, monotonic decline in species richness with increasing elevation might therefore be the general pattern for butterflies.

Species richness and density of majority of the sub-groups mirrored the overall richness and density patterns, however, there were few exceptions to this general pattern. Further, I also found that different groups of butterflies had different response to spatial, environmental and biotic variables. Differences between the groups clearly indicate that the perceived trends greatly depend on the subsets or the species taken into consideration (Wu et al., 2013b). The variations in trends and response to explanatory variables may be attributed to differences in physiological adaptation, ecological requirements, and evolutionary history of species groups (Wu et al., 2013b; Zang, 2019). Richness and density of families such as Nymphalidae, Papilionidae, Pieridae, Hesperiidae, and Lycaenidae followed a declining trend along elevation. Among these families, Hesperiidae and Papilionidae are mostly restricted to an elevation below 2000 m, probably due to physiological requirements for their energetic lifestyle. Similar trend has been observed by Acharya and Vijayan (2015) from the neighboring Teesta Valley in Sikkim). Riodinidae on the other hand did not follow any pattern simply because of very few species that are mostly restricted to the oak forest of the mid Himalayan range (Kehimkar, 2016).

Grouping the butterflies into range size categories revealed that the butterfly communities were mostly composed of a small-range species with majority restricted to a narrow elevational range. With a rise in elevation, the species richness and density of small-range butterflies decrease linearly, whereas large-range species do not display a consistent linear decline. Several studies have shown that environmental variables are likely to impact small-range species, whereas large-range species (with broader environmental tolerances) are influenced by geographical constraints and frequently exhibit a mid-range hump that matches the mid-domain effect (MDE) model (Jetz & Rahbek, 2001; Colwell et al., 2004; Brehm et al., 2007). Larger ranges are more likely to overlaps in the center of the domain creating a mid-elevation peak in richness (Colwell & Hurtt, 1994). A distinct mid-elevational peak in richness and density of the large-range species was observed in this study as well.

The Eastern Himalayan butterfly community were mainly dominated by Oriental species (mostly Indo-Chinese and Malayan forms) while there are less representation of Global and Palearctic components (Mani, 1974; Holloway, 1974). The Oriental species consists of species that are mostly adapted to the tropical hot/humid climate, whereas Palearctic elements have affinity to colder climatic regime (Holloway, 1974). Himalayan butterflies show a marked difference in niches occupied by the Palearctic and Oriental biota. The mixing of elements from different biogeographical affinities provides clear evidence that historical events such as continental drift, mountain uplift, and colonization were instrumental in shaping the current butterfly distribution in the Himalaya (Miehe et al., 2015).

Although there were distinct variations between several sub-groups in richness and density patterns, there were no differences in trends between butterflies classified according to their feeding specificity. The elevational niche-breadth hypothesis predicts that with increasing elevation, the diet breadth of herbivores increases (Rasmann et al., 2014), so it would be reasonable to conclude that a larger number of species will be polyphagous at higher elevations, whereas lower elevations will have more specialized species. The divergence in our findings from this hypothesis may be due to i) inadequate information on larval host plants for Himalayan butterflies, and (ii) the wide spatial extent of the alpine region (> 4000 m), which represents a stressful habitat and was not taken into account during the present research. In contrast to their lowland counterparts, animals in stressful environments are more likely to have complex life-history strategies. Nonetheless, there are mixed evidence for the niche-breadth hypothesis and shows great variation among different regions. Pellissier et al. (2013) demonstrated that the diet width of butterflies decreases with elevation in temperate climates, whereas the opposite trend was observed in the tropics by Rodríguez-Castañeda et al. (2010). Novotny et al. (2005) found no substantial difference in moth diet-breadth along the elevation in the tropics. Further research is required to understand how organisms are separated along environmental gradients (for example, elevation) in terms of their dietary requirements.

3.4.2 Determinants of butterfly species richness and density along the elevational gradient

Among all the variables, annual actual evapo-transpiration (AET) was the most significant factor influencing the overall species richness patterns and total density of butterflies along the elevation gradient in the present study. AET has been found to strongly determine the distribution pattern of butterflies (Acharya & Vijayan, 2015) and trees (Acharya et al. 2011b; Rana et al. 2019) along the elevation in the Eastern Himalaya. AET is known to decline with elevation (Trabucoo & Zomer, 2010) in the Eastern Himalaya and, hence, strongly correlates with the decline in species richness of butterflies. AET functions in two levels: (1) by directly influencing the physiology of organisms through temperature/light stress and water availability (water-energy balance or dynamics of water-energy) and (2) by affecting the ecosystem's net primary productivity (Rosenzweig, 1995; Hawkins & Porter, 2003a; Whittaker & Heegaard, 2003). Although both water-energy balance and the net primary productivity strongly influences diversity gradient of many taxa, the former has been demonstrated to be better explanatory model(Vetaas et al., 2019). Since butterflies are ectotherms, energy as temperature is crucial to butterflies for maintaining their basic physiology and wateravailability in all forms are important (nectars, mud puddles, fruit juices) since butterflies are liquid feeders (Haribal 1992; Fleishman et al., 2005; Kehimkar, 2008). Therefore, it can be inferred that AET influences species diversity both indirectly by affecting primary productivity and, most specifically by influencing the availability of water and energy and water. Large-range and Palearctic species, being widely distributed due to their higher level of environmental tolerance, are less affected by the AET gradients. Additionally, the density of majority of the butterfly sub-groups seemed less likely to be affected by the AET but more so by habitat variables indicating that resource abundance are necessary to maintain population of the species (Curtis et al., 2015).

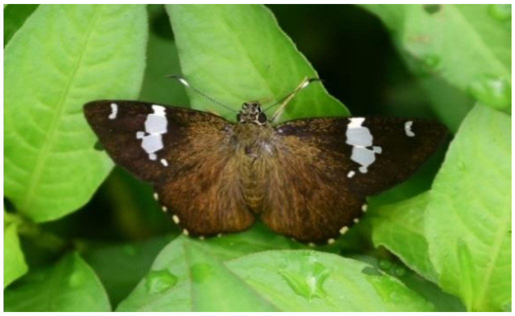
The availability of resources and the nature of habitat are also considered to be a strong determinant of species richness and density (Ribas et al., 2003; McCain & Grytnes, 2010). I found a close association between habitat variables (richness of the tree species, density of the tree, density of the shrub) and the pattern of species richness and density of butterflies and their sub-groups. Ambient climatic conditions (such as AET) promote vegetation growth by regulating the available resources such as water and energy (sunlight). Since butterflies are dependent on plants for their entire life cycle, the structure and composition of vegetation is critical in shaping butterfly distribution (Schulze et al., 2004; Vu, 2009). In particular, monophagous butterflies showed a close association with tree richness, suggesting that their distribution is mainly influenced by the distribution of host plants. In addition, it is clear that greater plant diversity results in a more heterogeneous ecosystem at lower elevation, causing an increase in the diversity of butterflies (Vetaas et al., 2019). Heterogeneity in habitat also affects the species richness because complex habitats provide more diverse resources, increasing the diversity of butterflies (Bazzaz, 1975).

Larger areas are known to harbor more number of species (Rosenzweig, 1992) due to the availability of more resources. In larger scale (regional or global), the rate of extinction rate decreases due to the presence of more population and speciation increases due to formation of potential barriers. In the local scale, larger area supports more diverse habitat for more species to thrive. Thus along the elevation gradient, species-area may function in between these two scales (Rosenzweig, 1995; McCain, 2007). However, in this study I did not find statistical significance of area as a potential driver of species richness and density of different sub-groups of butterflies. In contrary to most of the mountain areas where area decrease with increase in elevation, area in Sikkim Himalayan region shows two distinct peak (500 and 1500 m; Appendix 1) along the elevation. Similar findings were reported by studies in other parts of the Himalayan region where the relationship between area and species distribution did not show a significant relationship along the elevational gradient (Hu et al., 2017; Ding et al. 2019).

3.5 Conclusion

Species richness and density of butterflies declined linearly with increase in elevation in Rangeet valley in Sikkim, Eastern Himalaya. Highest number of species and abundance were recorded in the lower tropical valley below 500 m elevation making it the hotspot of butterfly diversity. Different butterfly sub-groups showed distinct pattern of species richness, and density. The associated factors also varied among different groups studied. Variation in observed trend of different groups indicates that same taxa may respond differentially to climatic changes and anthropogenic pressures. Since, species richness and density were mainly explained by climatic factors (including its determinants) and habitat variables, global climate change and habitat destruction will adversely affect butterflies in this region. Reports on range shift of butterflies due to global climatic changes are on rise (Forister et al., 2010; Braby & Hsu, 2019). More specifically, small ranged species, oriental species, majority of the butterfly families and polyphgaous species are likely to be effected by climate change. Monophagous species due to their exclusive dependency on habitat variables are also threatened by habitat destruction or alternation. Varied response of different groups to abiotic and biotic factors is mainly due to the difference in life history strategy. Hence, studies on life history traits are required to properly perceive the response different subgroups to the elevation.

Common Small Flat (*Sarangesa dasahara*)



Himalayan Spotted Flat (*Caelaenorrhinus munda*)

Striped Dawnfly (*Capila jayadeva*)

Tiger Hopper (*Ochus subvittatus*)

Himalayan Swift (*Polytremis discreta*)

Restricted Demon (*Notocrypta curvifasica)*

Potanthus sp

Figure-of-8-Swift (*Boaris pagana*)

Photo plate 3.1: Some representative butterfly species of Rangeet Valley (Family-Hesperiidae)

Orchid Tit (*Chilaria othona*)

Blue Imperal (*Ticherraacte*)

Lesser Grass Blue (*Zizina otis*)

Common Tinsel (*Catapacilma major*)

Powdery Green Sapphire (*Heliophorus tamu*)

Zebra Blue (*Leptotes plinius*)

Slate Royal (*Maneca bhotea*)

Straightwing Blue *(Orthomiella pontis*)

Photo plate 3.2: Some representative butterfly species of Rangeet Valley (Family-Lycaenidae)


Brown Prince (*Rohana parvata*)


Striped Blue Crow (*Eupolea mulciber*)


Common Castor (*Ariadne merione*)

Yellow Woodbrown (*Lethe nicetas*)

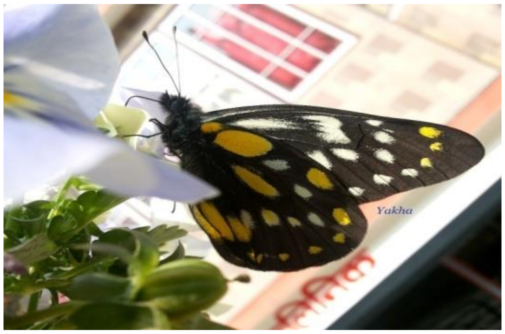

Staff Sergeant (*Athymas elenophora*)


Great Yellow Sailer (*Neptis radha*)


Knight (*Lebadea Martha*)


Green Commodore (*Sumalia daraxa*)

Photo plate 3.3: Some representative butterfly species of Rangeet Valley (Family-Nymphalidae)



Hill Jezebel (*Delias belladonna*)

Lesser Gull (*Ceporanadina*)

Dark Clouded Yellow (*Colias fieldii*)

Yellow Orange Tip (Ix*ias pyrene*)

Mottled Emigrant (*Catopsiliapyranthe*)

Tailed Sulphur (*Dercasverhuelli*)

Large Cabbage White (*Pieris brassicae*)

Psyche (*Leptosianina*)

Photo plate 3.4: Some representative butterfly species of Rangeet Valley (Family: Pieridae

Common Peacock (*Papilio bianor*)

Lesser Mime (*Papilioepycides*)

Common Mormon (*Papilio polytes*)

Common Windmill (*Byasa polyeuctes*)

Red Helen (*Papiliohelenus*)

Yellow Helen (*Papilio nephelus*)

Glassy Bluebottle (*Graphiumcloanthus*)

Great Jay (*Graphium eurypylus*)

Photo plate 3.5: Some representative butterfly species of Rangeet Valley (Family: Papilionidae)

Lesser Punch (*Dodona dipoea*)

Mixed Punch (*Dodna ouida*)

Punchinello (*Zemeros flegyas*)

Dark Judy (*Abisara fylla*)

Photo plate 3.6: Some representative butterfly species of Rangeet Valley (Family: Riodinidae)

CHAPTER 4

BETA DIVERSITY AND TRAIT ASSEMBLAGES OF BUTTERFLIES ALONG THE ELEVATIONAL GRADIENT

4.1. Introduction

Mountain regions are home to much of the world's terrestrial biodiversity (Spehn et al., 2010, Rahbek et al., 2019). In the vast mountain landscape, distribution of biodiversity varies with topography and changing climatic structure (McCain &Grytnes, 2010; Hendershot et al., 2017). There has been considerable upsurge in studies attempting to determine the pattern of biological diversity in the mountains and to understand its underlying mechanism, but such studies are often focused on alpha diversity (α; the number of species in a local community or particular elevational band) (Smith et al., 2007; Kumar et al., 2009; Rana et al., 2019). Beta (β) diversity might also vary with elevation (Whittaker, 1960) and understanding the patterns and determinants of β-diversity provide insights one factors that shape community structure (Kraft et al., 2011) andpatterns of α-diversity across sites (da Silva et al., 2018a). Such studies would also aid in indentifying areas that can be prioritized for conservation (Jankowski et al., 2009; Gomes et al., 2020)

Beta diversity is defined as the variation in species composition assemblages among different sites (Anderson et al., 2011) and provides the link between α-diversity at local scales and gamma (γ)diversity at regional scales. Along elevational gradients, beta diversity declines with elevation (Kraft et al., 2011), peaks at mid-elevations (Hu et al., 2018; Naud et al., 2019) or even increase with elevation (Syfert et al., 2018; Castro et al., 2019). The variability in the pattern is largely due to the differences in ecology of taxa considered and region where the research was undertaken (Sanders & Rahbek, 2012). However, it is certain that the beta diversity significantly increases with increase in elevational distance between the sites.

The beta diversity encompasses two antithetical processes; turnover and nestedness (Baselgaet al., 2010; Baselga, 2013). The turnover component of beta diversity reflects the phenomena of species replacement by other species from site to site or habitat to habitat (Baselgaet al., 2010).On the other hand, nestedness occurs when species are lost from one site to the other as a result of random processes that causes disaggregation of species e.g colonization and extinction. The balanced variation in abundance based dissimilarity is equivalent to the turnover component (incidence based variation), as individuals of one species are substituted by individuals of other species form site to another (Baselga, 2013). The abundance gradient on the other hand complements the nestedness component in the incidence based variation as the individuals are replaced without substitution. Disentangling the components of beta diversity aids in formulating distinct conservation strategies e.g. if turnover is high then it would require larger number of distinct areas to be conserved but if a nestedness is dominant then few areas but with high species richness would have to be prioritized for conservation (Baselga, 2010).Much of the available literature suggests that turnover is the major cause of variation in species assemblages along elevational gradients as a result of abrupt abiotic changes (Jiang et al., 2019), whereas relatively few studies have found nested structure in speciescompositional dissimilarity along elevational gradients (Patterson et al., 1996; Presley et al.,2012).

Several models have been proposed to explain the variation in beta diversity. The "*niche based model*" emphasizes on the environmental filtering and niche partition in shaping the species assembly mechanism (Whittaker, 1956;Legendre et al., 2005). The model states that the landscapes are mosaics with distinct environmental characteristic which determine the assemblage of species communities that are adapted to that environmentSeveral other studies have recognized the role of spatial factors such as geographic distances in assemblage dissimilarity; better known as "*neutral model*" (Bell, 2001; Legendre et al., 2005). The neutral hypothesis highlights the importance of historical factors such as colonization and speciation processes as well as dispersal capacity of taxa in determining the assemblage composition of an ecological community. Since both environmental sorting and neutral processes may work complementarily in structuring a ecological community, determining the relative effect of both is important (Leibold et al., 2004, da Silva, 2018a).

Environmental variation significantly affects butterfly traits such as dietary specialization, elevational range, biogeographic position, wingspan, etc (Barbaro & van Halder, 2009;Kaltsas et al., 2018). Species having similar traits tend to co-occurring habitats with similar environmental condition (Leingärtner et al., 2014). When environmental conditions change, a community-level trait values also change, typically as a result of species turnover (Cornwell & Ackerly, 2009). Hence, studying traits along gradients are crucial in understanding mechanisms of community assembly and the responses of species to environmental variation. The responses of species or communities to environmental variation are thought to mirror the effects of climate change (Hodkinson, 2005). Studies along the environment gradients can be used as a space-for-time substitute for understanding the effect of climate change on communities (Dunne et al., 2004; Sundqvist et al.,2013).

Studies on elevational pattern of biodiversity in the Himalayan region (Acharya et al., 2011a; Acharya et al., 2011b; Bhardwaj et al., 2012; Acharya& Vijayan, 2015;Rana et al., 2019) have mainly focused on patterns in alpha diversity; studies on beta diversity and trait variation, and what they can indicate about mechanisms, are still very scarce (but see Tonkin et al., 2017; Hu et al., 2018) and to our knowledge none exist for butterflies in the Himalaya. In this study, I describe the pattern of beta diversity (both incidence and abundance based) of butterflies along the elevational gradient in Rangeet Valley, Eastern Himalaya, India. I partitioned beta diversity into its additive components (turnover, nestedness, balance variation and abundance gradient). I also determine how beta diversity and its components vary with increasing in elevational distance between sites. I used generalized dissimilarity modeling (GDM) analysis to determine the underlying mechanism affecting the beta diversity pattern. Lastly, I analysed the effect of environmental gradients along the elevation on trait composition of butterflies along the elevational gradient.

4.2Materials and methods

4.2.1 Study area

The present study was conducted along the elevational gradient in Rangeet Valley, Sikkim, Eastern Himalaya. For this study total elevational range of 3300m (300m-3300m) was selected. A detail of the study area is provided in Chapter 2.

4.2.2 Butterfly sampling

Fixed width point count (radius = 5m) along a permanent transect (length = 1000 m) was used for sampling butterflies (Acharya & Vijayan, 2015). Along the entire extent of study area (300-3300 m), 16 transects were established. In each transect, a total of 10 permanent points were laid. A comprehensive detail of the sampling method is provided in Chapter 3.

4.2.3 Traits and species groupings

Butterfly traits such as range size, wingspan, larval host plant specialization and biogeographic affinity were considered in this study (**Table A.2**). The traits values were assigned to each individual in accordance to the criteria that has been discussed in Chapter 3. Data on wingspan of butterflies were obtained from Kehimkar (2016). .Range size was considered as a difference between highest and the lowest elevational range from where a butterfly species was recorded. Each butterflies were assigned having affinity to i) Global (ii) Oriental, iii) Palearctic and iv) Afro-tropical biogeographic region. In terms of host plant specialization butterflies were categorized as i) monophagous, ii) oligophagous, and iii) polyphagous species (Zhang et al., 2019; Dewan et al., 2021). In cases of unavailability of information on traits, data for genus and family was extrapolated to species level.

4.2.4 Predictor variables

Actual Evapotranspiration (AET), Normalized Difference in Vegetation Index (NDVI), tree richness, tree density, shrub richness and density was used as environmental predictor of beta diversity. Details about sampling methods and estimation of each predictor variables are provided in Chapter 3.

4.2.2Data analysis

In order to estimate pairwise beta diversity of butterflies along elevation gradient, both incidence and abundance based beta diversity measures were used (Baselga, 2010). Sorenson dissimilarly index (β_{sor}) was calculated as the total pairwise incidence based beta diversity. The total incidence based dissimilarity was partitioned it into nestedness (β_{nes}) and turnover components (β_{sim}). Turnover represents the species replacement phenomena while the nestedness constitutes the species loss mechanism. Since the incidence based dissimilarity doesnot consider abundance of species, the rare and common species will be treated as similar samples. Additionally, bias correction and variation estimation are impossible with only incidence based data (Chao et al., 2006). Hence, in order to compensate biases associated incidence based estimates, I also calculated abundance-based beta diversity as Bray-Curtis dissimilarity index (d_{BC}). The total abundance based dissimilarity (d_{BC}) was then partitioned into balanced variation ($d_{BC\text{-}bal}$) and abundance gradient components ($d_{BC\text{-}gra}$) following Baselga (2013). Similar to the turnover component, the balanced variation ($d_{BC\text{-}bal}$) represents the substitution of individuals of one species by the same number of individuals but of other species form site to site. The abundance gradient, on the other hand, is complementary to the nestedness component and occurs when individuals are lost form one site to another without the species being replaced. To assess the pattern of beta diversity along the elevational gradient, overall dissimilarity (both incidence and abundance based) and its component between each pair of adjacent elevational sites/bands was estimated using linear and quadratic regression models. Pair-wise dissimilarity (turnover/balanced variation and nestedness/abundance gradient) for every pair of elevational bands was also estimated. The values of pair-wise dissimilarity were plotted against elevational distance between different elevational zones. For this analysis, elevational distance matrix was created using Euclidean distance approach using Pearson's correlation to test the correlation of overall dissimilarity and its components with the elevational distance. The significance of correlation was tested using Mantel test. All the analysis was conducted in R software software (version 3.4.3) using *vegan* (Oksanen et al., 2016) and *betapart* (Baselga & Orme, 2012) packages. $\beta_{sor}$and d_{BC} dissimilarity values of each elevational zone was used as a distance matrix to generate a dendrogram plot through hierarchical clustering. Cluster analysis was conducted in R software software (version 3.4.3) by using the function "*hclust*".

Generalized dissimilarity modeling (GDM) analysis was conducted in order to understand the effect of space and environment on the compositional dissimilarities of butterflies along the elevational gradient. The GDM is a type of linear matrix based regression that models compositional dissimilarity between pairs of sites in relation to the environmental and geographic distance (Ferrier et al., 2007). Non-linearity in ecological datasets arises mainly due to- i) curvilinear relationship between compositional dissimilarity and increasing environmental distance, ii) rates of turnover along the environmental gradients which often is non-stationary. The GDM first transforms the predictor variables using maximum likelihood and flexible I-splines in order to provide the best supported relationship between biotic dissimilarities and environmental/geographic distance. The GDM then accounts for curvilinearity by transforming the scaled and combined distance using a log link function. I used dissimilarity matrices and site-by-environment matrices(where sites represent each elevational zones), to fit GDMs. I considered Actual Evapotranspiration (AET) as an environmental predictor along with other biotic variables such as tree species richness (TSR), tree density (TRD), shrub species richness (SSR), shrub density (SD) and Normalized Difference Vegetation Index (NDVI) for analysis. I used geographic coordinates for calculating geographic distance of the sites in each elevational zone. I tested the importance of each predictor variable and plotted their I-splines. The GDM analysis was conducted in R software using '*gdm*' package (Manion et al., 2017). Finally, I partitioned the deviance in the *gdm* model following Borcard et al.(1992).

I used a combination of RLQ (Dolédec et al., 1996) and Fourth-corner analysis (Legendre et al., 1997) to investigate the effect of environmental and biotic variables on butterfly traits. Both the methods are based on the coinertia analysis between sets of three matrices; R (site *x* environment table matrix is a site *x* species table,), L (matrix is a site *x* species table), Q (traits data of the species matrix is a species *x* trait table). In order to compensate for the skewed dataset caused by different traits having different measurements, all the variables were log transformed prior to the analysis. For species-level data Hellinger transformation was used (Legendre & Gallagher, 2001). I first applied separate ordination to the R, L and Q matrices. I then related the Q and R matrix using L as the link. This analysis creates a fourth matrix (Environment x Traits) which is used to summarize the joint structure of the three matrices (Dray et al., 2014).I applied Principal Component Analysis (PCA) ordination of the R matrix (log transformed). As Q matrix contained a mixed data, I used Hill/Smith PCA analysis (Hill & Smith, 1976). For the ordination of L matrix I used Correspondence Analysis (CA). The fourth-corner method was combined inorder to test the hypothesis of RLQ ordinations.The fourth-corner analysis specifically test the significance of the correlation observed in species traits or environmental variables in the RLQ ordination axes (Dray et al., 2014). The significance of correlation was tested by conducting 999 permutations and referring to p values adjusted through the false correction method (Benjamini& Hochberg, 1995). Both the RLQ-Fourth corner analyses were conducted using package *ade4* (Dray & Dufour, 2007) in R software.

4.3 Results

4.3.1 Patterns of beta diversity along the elevation gradient

The mean pair wise dissimilarity for β_{sor} (incidence based) and d_{BC} (abundance based) along the elevation gradient of Rangeet Valley was 0.735and 0.794 respectively (**Table 4.1**). β_{sim} (turnover component) greatly contributed to the overall beta diversity as compared to β_{nes} (nestedness component). The average β_{sim} and β_{nes} of the butterfly community were 0.600 and 0.135 respectively. Similar pattern was observed in case of abundance based dissimilarity were $d_{BC\text{-}bal}$(balance variation) with mean value of 0.693 was a major contributor of abundance dissimilarity than the $d_{BC\text{-}gra}$(abundance gradient) with mean value of 0.101. Both incidence and abundance based dissimilarity between two adjacent sites along the elevation revealed two peaks, one between 950-1150 m and other between 2100-2300 m (**Table 4.2**; **Figure 4.1).** The quadratic models, indicating a hump-shaped pattern performed better the than linear models in explaining the beta diversity trend along the elevation gradient (**Table 4.3**). At mid elevation, β_{sor}, $\beta_{sim,}$ $_{dBC}$and $d_{BC\text{-}bal}$ were significantly higher than at the low or high elevation sites. No significant elevational trend was observed in case of $\beta_{nes}$and $d_{BC\text{-}gra}$.

Table 4.1: Mean value, standard deviation (SD), minimum(Min) and maximum range(Max) of the overall incidence based (βsor) and abundance based (d_{BC}) dissimilaritiesof butterflies and their substitution components inRangeet Valley, Sikkim, Eastern Himalaya.

	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

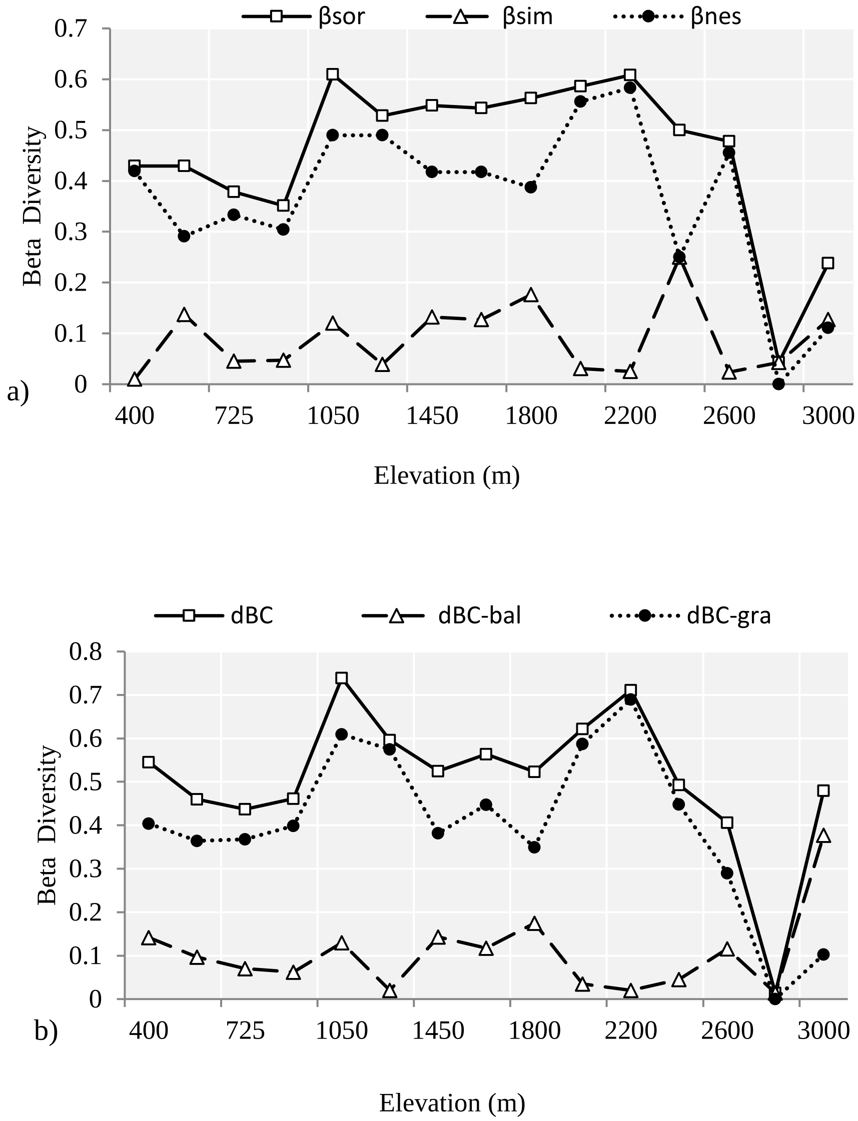


Figure 4.1: Pairwise a) incidence based and b) abundance based beta diversity of butterflies between two adjacent sites along the elevation gradient in Rangeet Valley, Sikkim, Eastern Himalaya. β_{sor}(Sorenson dissimilarity index); β_{sim} (turnover); β_{sim} (nestedness) ; d_{BC} (Bray-Curtis dissimilarity index) ; $d_{BC\text{-}bal}$ (balanced variation); $d_{BC\text{-}gra}$ (abundance gradient).

Table 4.2: Values of total beta diversity and its additive components between adjacent zones of elevation in Rangeet Valley, Sikkim, Eastern Himalaya. Beta diversity is measured as (a) Sorenson dissimilarity index (β_{sor}), its turnover (β_{sim}), and nestedness (β_{nes}) components; (b) Bray-Curtis dissimilarity index (d_{BC}) its balanced variation ($d_{BC\text{-}bal}$) and abundance gradient ($d_{BC\text{-}gra}$) components.

Elevation (m)	β_{sor}	β_{sim}	β_{nes}	d_{BC}	$d_{BC\text{-}bal}$	$d_{BC\text{-}gra}$
350-500	0.429	0.010	0.419	0.545	0.142	0.404
500-650	0.429	0.137	0.291	0.460	0.097	0.364
650-800	0.378	0.045	0.333	0.437	0.070	0.368
800-950	0.351	0.047	0.304	0.461	0.062	0.399
950-1150	0.609	0.120	0.490	0.739	0.130	0.609
1150-1350	0.528	0.039	0.490	0.596	0.020	0.575
1350-1550	0.548	0.132	0.417	0.525	0.143	0.382
1550-1700	0.543	0.127	0.417	0.564	0.117	0.447
1700-1900	0.563	0.176	0.387	0.523	0.175	0.349
1900-2100	0.586	0.031	0.556	0.622	0.035	0.587
2100-2300	0.608	0.025	0.583	0.711	0.020	0.690
2300-2500	0.500	0.250	0.250	0.493	0.045	0.448
2500-2700	0.478	0.024	0.455	0.406	0.116	0.290
2700-2900	0.043	0.043	0.000	0.014	0.014	0.000
2900-3100	0.238	0.127	0.111	0.480	0.377	0.103
Mean dissimilarity	0.456	0.089	0.367	0.505	0.104	0.401

Table 4.3: Linear and quadratic models showing relationship of incidence based (β_{sor}) and abundance based (d_{BC}) dissimilarity measures and their additive components with elevation.

	Models	**R^2**	**Pr(>|t|)**	**AIC**
B_{sor}	~ 5-(5.086-05) Elevation + 0.539	0.075	0.323	-9.627
	~ -1.565^{-14}Elevation^2+1.103^{-07} Elevation+ 0.328	0.656	**0.002**	-20.36
B_{sim}	~-6.374-^{05} Elevation+ 0.472	0.112	0.222	-9.460
	~ -1.395^{-14} (Elevation)^2 + 9.324^{-08} Elevation+0.319	0.571	**0.006**	-16.01
B_{nes}	~ 1.289-^{05} Elevation + 0.067	0.238	0.583	-8.061
	~ -1.702-^{15} Elevation^2+ 1.710^{-08}Elevation+ 0.063	0.041	0.780	-10.33
d_{BC}	~ -6.485^{-05} Elevation +0.612	0.063	**0.024**	-24.87
	~ -8.765^{-15}Elevation^2 + 5.044^{-08}Elevation+ 0.502	0.041	**0.014**	-10.33
$d_{BC\text{-}bal}$	~ -8.624^{-05} Elevation + 0.543	0.1561	0.145	-6.128
	~ -1.958^{-07} (Elevation)^2+ 5.767^{-04}Elevation+ 0.109	0.550	**0.009**	-28.11
$d_{BC\text{-}gra}$	~ 2.140-05 Elevation+ 0.068	0.038	0.485	-24.87
	~ 6.604-15 (Elevation)^2-4.738^{-08}Elevation + 0.137	0.321	0.098	-25.55

R^2 = proportion of variance explained; Pr(>|t|) = level of significance ($p < 0.05$) measuring level of significance; AIC = Akaike Information Criteira. Significant models ($p<0.05$) are marked in bold. β_{sor} (Sorenson dissimilarity index); β_{sim} (turnover) ; β_{nes} (nestdessness) ; d_{BC} (Bray-Curtis dissimilarity index) ; $d_{BC\text{-}bal}$ (balanced variation); $d_{BC\text{-}gra}$ (abundance gradient).

Cluster analysis revealed that the butterfly communities of low and mid elevation were distinct from their high elevation counterparts (**Figure 4.2**). Based on Mantel tests, pairwise incidence based beta diversity- β_{sor}($r = 0.8226$, $p < 0.01$), β_{sim}($r = 0.76$, $p < 0.01$) and β_{nes}($r = 0.21$, $p < 0.05$)increased significantly with an increase in elevational distance between the sites (**Figure 4.3**). Similarly, the abundance based beta diversity d_{BC}($r = 0.80$, $p < 0.01$) and $d_{BC\text{-}bal}$ ($r = 0.74$, $p < 0.01$) also increased significantly with rising elevational distance. However $d_{BC\text{-}gra}$ ($r = -0.23$, $p = 0.986$) did not show any significant correlation with the elevational distance along the gradient.

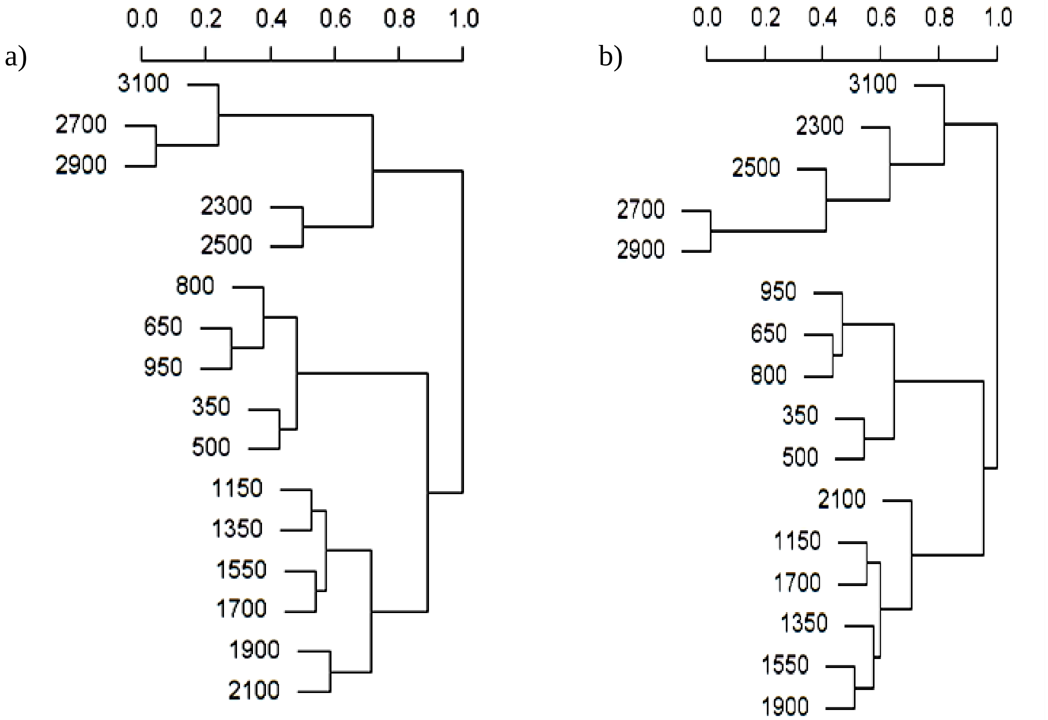
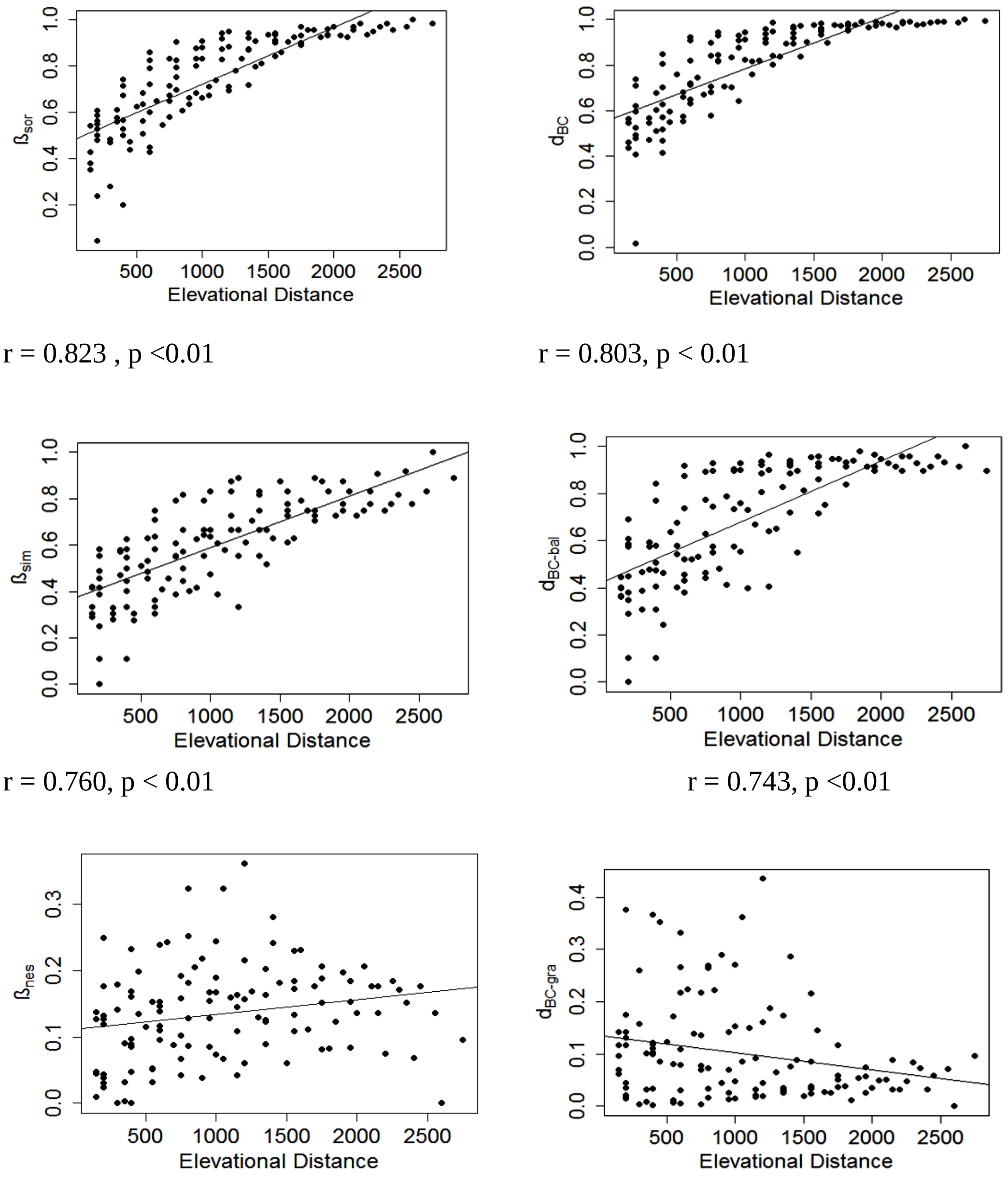


Figure 4.2: Dendrogram based on a) incidence based Sorenson dissimilarity index (β_{sor}) and b) abundance based Bray-Curtis dissimilarity index of butterfly assemblage in different elevation zones in Rangeet Valley, Sikkim, Eastern Himalaya.



r = 0.823 , p <0.01

r = 0.803, p < 0.01

r = 0.760, p < 0.01

r = 0.743, p <0.01

r = 0.211, p <0.05

r = -0.239, p = 0.986

Figure 4.3: 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}) its turnover (β_{sim}) and nestdessness (β_{sim}) components; (b) Bray-Curtis dissimilarity index (d_{BC}) its balanced variation ($d_{BC\text{-}bal}$) and abundance gradient ($d_{BC\text{-}gra}$) components.Pearson correlation coefficient (*r*) and significance (*p)* value computed using Mantel tests are also shown.

4.3.2 GDM and deviance partitioning

Generalized dissimilarity model showed AET, tree richness, tree density and geographic distance as the significant predictors of $\beta_{sor.}$ Among all these variables, AET was the most important predictor for beta diversity measures (**Table 4.4; Figure 4.4)**. The full GDM model explained about 88.03%, pure environmental variables alone explained 87.8%, while geographic distance explained only about 0.001% of the total deviance observed in the model. The combined deviance of environmental variables and geographic distance was only 0.21%. Similarly, in case of β_{sim}, AET, tree richness, tree density and geographic distance was found to be the best predictors. The full model contributed about 76.8% of the deviance observed while environmental variables explained 76.1%, geographic distance explained 0.13%, and only 0.23% of the total deviance was shared by these two factors. Only AET was found to be a significant predictor for β_{nes}. Environmental variable explained only 7.39 % deviance observed in the model while geographic distance did not have any contribution.

In case of d_{BC} and $d_{BC\text{-}bal}$, AET was the most important predictor followed by, tree richness, tree density and geographic distance**(Table 4.4; Figure 4.5)**. These variables explained about 86.77% and 81.00% of the deviance observed in d_{BC} and $d_{BC\text{-}bal}$ respectively. Environmental variables independently explained about 86.65% of deviance, and geographic distance explained 0.36 % of deviance observed in $d_{BC,}$ while 0.23% was jointly shared (**Figure 4.6**). Likewise in the case of$d_{BC\text{-}bal}$, environmental variables and geographic distance respectively explained 80.81% and 0.11% of the deviance observed and 0.0758% of the total deviance in $d_{BC\text{-}bal}$was jointly shared. . In contrary, GDM with shrub density and geographic distance was found to be the best fit for $d_{BC\text{-}gra}$. .However, these variables explained only 11.62% of the deviance observed in case of $d_{BC\text{-}gra}$.

Table 4.4: Summary of Generalized Dissimilarity Models showing relationship between incidence based (βsor) and abundance based (d_{BC})dissimilarity of butterflies in Sikkim, Eastern Himalaya and their additive components with environmental variables and geographic distance.

	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
AET	**46.420**	**43.461**	**46.430**	**40.147**	**35.398**	0.832
TSR	**3.550**	**4.246**	5.063	**5.518**	**9.093**	0.000
TRD	**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
SSD	0.606	0.802	0.000	**0.845**	0.045	35.837
NDVI	0.743	0.527	12.157	0.201	0.213	5.829

Significant variables are marked in bold ($p< 0.05$). β_{sor} (Sorenson dissimilarity index); β_{sim} (turnover) ; β_{nes} (nestdessness) ; d_{BC} (Bray-Curtis dissimilarity index) ; $d_{BC\text{-}bal}$ (balanced variation); $d_{BC\text{-}gra}$ (abundance gradient); AET (Actual Evapotranspiration); TSR (Tree Species Richness); TRD (Tree Density); SSR (Shrub Species Richness); SSD (Shrub Density);NDVI (Normalized Difference Vegetation Index).

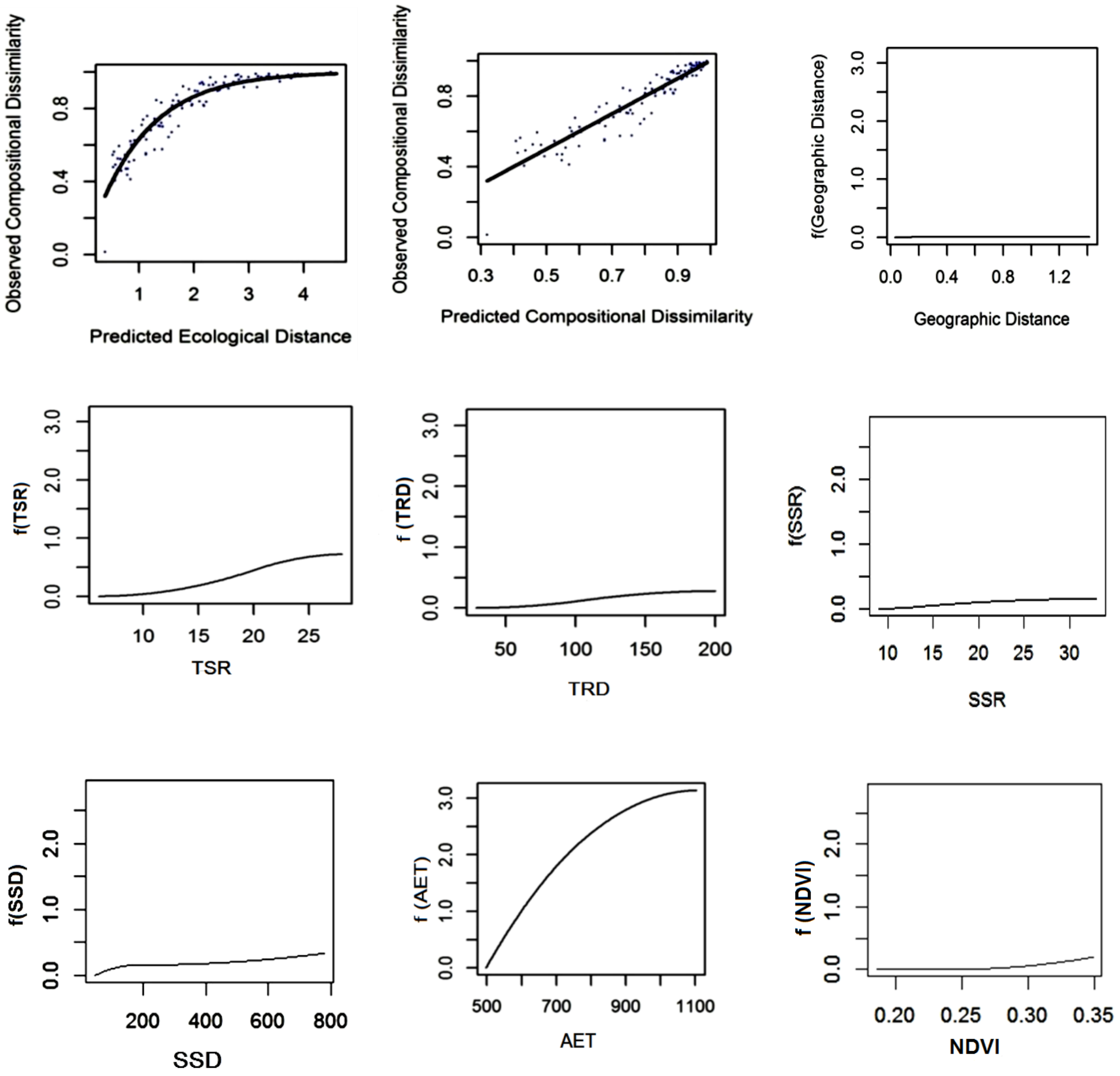


Figure 4.4: Generalized dissimilarity model fitted I splines for variables affecting the incidence based dissimilarity (β_{sor}) of butterflies in Rangeet Valley, Sikkim, Eastern Himalaya. TSR (Tree Species Richness); TRD (Tree Density); SSD (Shrub Density); SSR (Shrub Species Richness); AET (Actual Evapotranspiration); NDVI (Normalized Difference Vegetation Index)

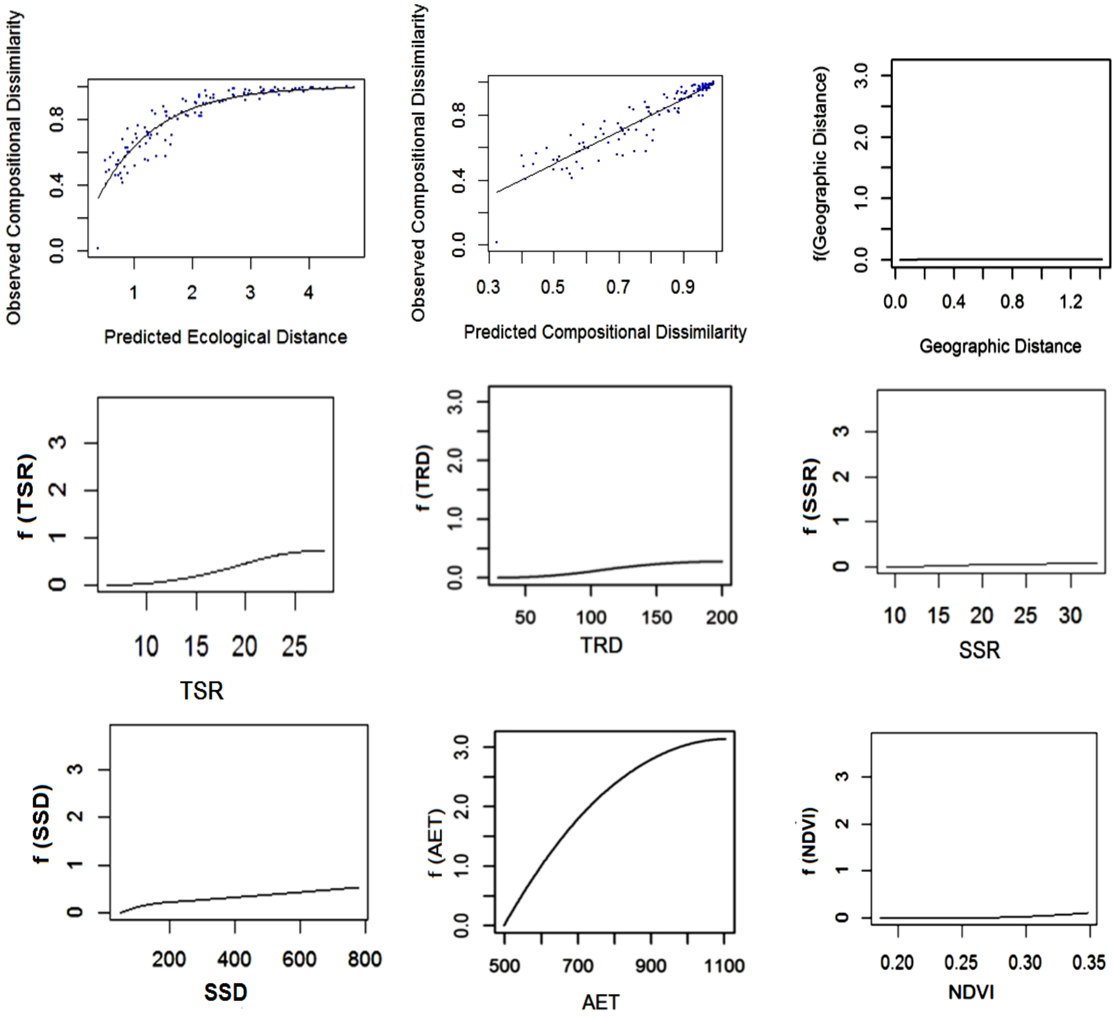


Figure 4.5: Generalized dissimilarity model fitted I splines for variables affecting the abundance based dissimilarity (d_{BC}) of butterflies in Rangeet Valley, Sikkim, Eastern Himalaya. TSR (Tree Species Richness); TRD (Tree Density); SSD (Shrub Density); SSR (Shrub Species Richness); AET (Actual Evapotranspiration); NDVI (Normalized Difference Vegetation Index)

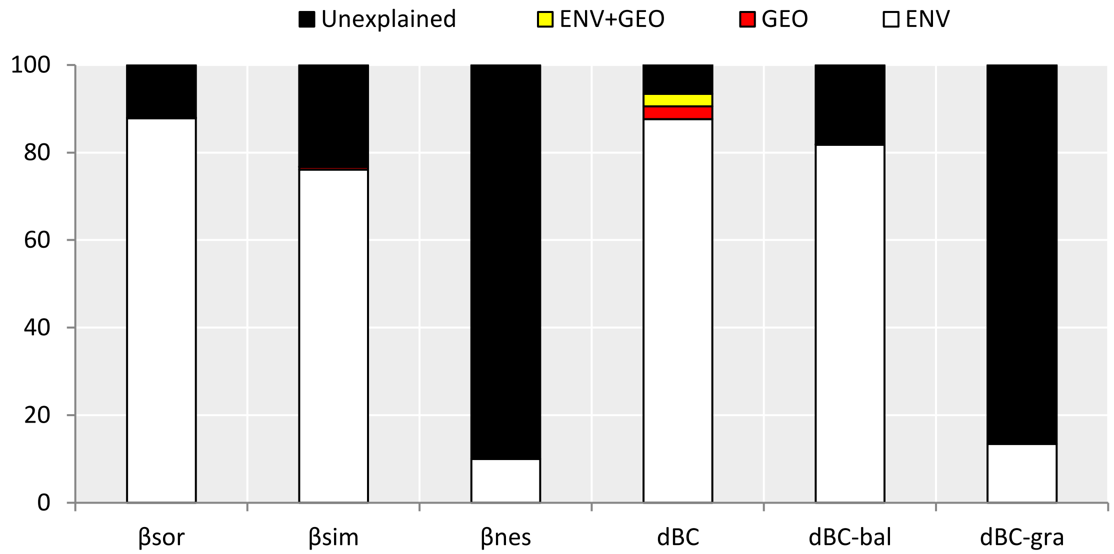


Figure 4.6: Proportion of deviance (shared and independent) of the generalized dissimilarity model (GDM) explained by the environmental predictors (ENV) and geographic distance (GEO) in explaining Sorenson dissimilarity index (β_{sor}) its turnover (β_{sim}) and nestdessness (β_{sim}) components and Bray-Curtis dissimilarity index (d_{BC}) its balanced variation ($d_{BC\text{-}bal}$) and abundance gradient ($d_{BC\text{-}gra}$) of butterflies along elevation gradient in Sikkim, Eastern Himalaya.

4.3.3 Trait composition of butterfly community

RLQ analysis showed overall significant association of traits variation in butterflies, elevation and environmental variables (Monte-Carlo permutation test; nrepeat= 49999; $p < 0.05$). About 98.51% of the total variation observed in RLQ plots was explained by first two axesalone (**Table 4.5**). The combined RLQ and fourth corner analysis showed significant negative association of environmental variables such as AET, tree density and tree richness with the first axis (**Table 4.6; Figure4.7**). The first axis projects the changes in gradient of environment from warm and humid tropical lower elevation to more harsh and dry environments in the higher elevation. The axis also relates to reduction of the tree richness and density in the higher elevation. Butterflies having Palearctic affinity were positively correlated to the first axes, whereas no other butterfly traits showed any significant correlation with any other axes.

Table 4.5: Summary of the RLQ analysis. Details of the eigenvalues, correlation, percentage of the total projected inertia of the explained by first two axis, percentage variance retained by R (environmental variable matrix), percentage variance retained by L (species matrix) and percentage variance retained by Q(species traits matrix) are provided.

	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

Table 4.6: Combination of fourth-cornerand RLQ results showing the relationship betweenbutterfly traits and environmental variables. a) Fourth-cornertests 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.

a) Butterfly traits	**Axis R1**	**Axis R2**	**b) Environmental Variables**	**Axis Q1**	**Axis Q2**
Range Size	0.167	-0.116	TSR	**-0.265**	-0.156
Bio_A.AT	-0.065	-0.828	TRD	**-0.223**	-0.061
Bio_A.GL	-0.046	0.049	SSR	-0.0894	-0.099
Bio_A.OR	-0.114	-0.131	SSD	-0.188	0.141
Bio_A.PA	**0.272**	0.129	AET	-0.389	0.059
Polyp.MO	0.036	-0.118	NDVI	0.115	-0.124
Polyp.OL	0.143	0.001			
Polyp.PL	-0.189	0.050			
Wingspan	-0.123	-0.038			

Significant associations are marked in bold (adjusted p< 0.05). TSR (Tree Species Richness); TRD (Tree Density); SSD (Shrub Density); SSR (Shrub Species Richness); AET (Actual Evapotranspiration); NDVI (Normalized Difference Vegetation Index); 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).

Figure 4.7: Results of RLQ analysis of butterflies showing scores of (a) sites, (b) species (c) environmental variables and (d) traits. In (a) elevation in meters. In (b) species represented by species code numbers. In (c) TSR (Tree Species Richness); TRD (Tree Density); SSD (Shrub Density); SSR (Shrub Species Richness); AET (Actual Evapotranspiration); NDVI (Normalized Difference Vegetation Index). In (d) 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).

4.4 Discussion

4.4.1 Beta diversity pattern of butterflies along the elevational gradient.

Here I studied the pattern in beta diversity and community-level traits of butterflies along an extensive elevational gradient in the eastern Himalaya. I found that the trends in incidence based dissimilarity were similar to the trends observed in abundance based dissimilarity. Hence, each one of the measures could be used complimentarily in explaining the beta diversity trends of butterflies in the mountains. The overall composition of butterflies across the elevational zones in the entire landscape showed high dissimilarity (73.5% β_{sor} and 79.4% d_{BC}). The turnover (incidence based dissimilarity) or the balanced variation (abundance based dissimilarity) explained most of the dissimilarity in butterfly community indicating that one assemblage of species and its populations are being replaced by different populations in other elevation sites (Baselga, 2010; Baselga, 2013).Similar results were obtained from the other mountain regions for a wide variety of taxa, such as plants (Zhao et al., 2019), soil Enchytraeidae (Jiang et al.,2019), dung beetles (da Silva et al., 2018b) and ants (Flores et al., 2018). High levels of substitution of species and its population components indicate that the assemblages of butterflies are relatively unique along the elevational gradient examined here. Hence, the high regional diversity of butterflies in the Himalaya arises mainly because of rapid turnover among communities.

Beta diversity donot show a general trend along the elevation but varies with taxa and region. Similar to the trends in beta diversity of the Himalayan butterflies (Acharya &Vijayan, 2015) and birds (Hu et al., 2018) I found a hump-shaped pattern with a peak at the mid elevation. The edge effect phenomena which occur in the ecotone boundaries between adjacent sites in the mid elevation possibly contributed to high beta diversity observed in the present study (Despland et al., 2012). In mountains, the ecotone boundaries separate different vegetation zones. The ecotone boundary between tropical semi-deciduous forests and sub-tropical broad-leaved forests at 900-1150m in the Sikkim Himalaya (Haribal, 1992), coincides with the peak in beta diversity observed during the current research. Another peak in beta diversity occurs in the transition zone of subtropical forests and dense temperate broad-leaved forest (between 2100 and 2300 m). Changes in butterfly assemblages at ecotonal boundaries (or vegetation transition zones) are commonly observed in mountainous areas, and have been previously recorded from Northern Chile (Despland et al., 2012) and Northern Israel (Kent et al., 2013).

The total beta diversity of butterflies increased significantly with increase in elevational distance between the sites. The data indicates that the increase in incidence based beta diversity was mainly due to the increase in turnover rate and abundance based beta diversity was associated mainly with the substitution of abundance of species assemblage. High substitution of butterfly assemblages gives direct evidence that the communities in high elevations are not the subset of lower elevations. Cluster analysis reveals that the low and mid elevation formed separate cluster distinct to the high elevation. Such phenomena commonly occur in pristine mountain landscapes where environment filters species into local assemblages, making each elevation zone unique on its own (Kaltsas et al., 2018; Jiang et al., 2019).

4.4.2 Determinants of beta diversity along the elevational gradient.

Along any ecological gradients,two important phenomenon -environmental filtering and spatial constraints- basically influence the pattern of species community assemblages (Legendre et al., 2005). The environmental variables explained most of the variation in the beta diversity pattern of butterflies in Sikkim Himalaya. The results in this study confirm to "*niche based model*" or "*speciessorting model*", which illustrates the strong effect of environmental factors in a particular habitat in shaping the species composition of butterflies (Whittaker, 1956). Similar to our finding, studies across several taxa has reported the environmental factors explaining the large proportion of variation in beta diversity (Jankowski et al., 2009; Jiang et al., 2019; Hu et al., 2018; López-Delgado et al., 2019). In contrary, few argues the importance of spatial "*neutral processes*" such as spatial distances that limits the dispersal of a species resulting into higher dissimilarity among sites located farther apart (Bell, 2001). Nonetheless, ecologists do agree that combined effect of environmental and spatial processes on species distribution is the fundamental basis of how an ecological community is structured in a given habitat or location (Leibold et al., 2004; Legendre et al., 2005).

Among the set of environmental variables, differences in AET, tree richness, and density among different elevational zone had the largest effect on beta 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 ecosystem (Hawkins & Porter, 2003a). Butterflies depend largely on thermal energy for maintaining their physiology, and water availability as the food resources (in the form of nectars, mud puddles, fruit juices) since butterflies is dominantly liquid feeders (Fleishman et al., 2005).Diversity of plants in the habitat also influences the distribution of animals at local level (Siemann et al., 1998; Haddad et al., 2001). However, at larger geographical scales, herbivores show more affinity to climate rather than plant at the regional level (Hawkins &Porter, 2003b). Hawkins and Porter (2003b) demonstrated the correlation of plants and butterfly distribution at moderate scales, but once the water-energy balance (AET) and topographic variables were added in a regression model, the effect if plants were non-significant. Butterflies and plants respond *synchronously* to the changes occurring in the climate regime in the Rangeet Valley. The ambient climatic conditions (such as AET) provide resources that facilitate the growth of more vegetation. AET has been found to be a strong predictor of tree diversity along the elevation in the Eastern Himalaya (Acharya et al., 2011a; Rana et al., 2019). The vegetation types in turn determine butterfly communities that are ultimately adapted to such habitats. Habitat diversity and structure such as plant richness, understory coverage, canopy openness and basal area influences the assemblage pattern of butterflies in range of ecosystem types (Sharma et al., 2020). AET is known to decrease linearly with the elevation (Trabucco & Zomer, 2010). In the Eastern Himalaya, the rapid transition of AET coupled with vegetation changes creates a climate-habitat gradient along the elevation. The lower elevations being warmer provides heterogeneous habitat, productive environment and supports a diverse group of butterfly community. The butterfly communities on the higher elevation are characterized by few but unique species. Here, the cold and harsh environment favors only few species evolved with specialized trait to thrive in those niches.

4.4.3 Trait composition of butterflies along the elevational gradient

The apparent niche division between the butterflies along elevation is perhaps largely due to their historical affinities toward the biogeography realms. Based on the distribution ranges and centers of diversity, Holloway (1974) categorized butterflies according to their affinities with different biogeographical realm. In the Himalayan region, most of the species occurring in the low-mid elevation have affinity to oriental realms (Indo-Malayan or Indo-Chinese) and are adapted to the tropical hot/humid climate, whereas the high elevation butterflies are composed of Palearctic elements adapted to colder temperate region(Mani, 1974;Holloway, 1974; Haribal, 1992). However, few Oriental species also have their distributional ranges to extend to region of high elevation. The colonization of butterflies in the colder climatic regimes is due to the deviance from their niche conservatism (DeVries, 2000; Hawkins &DeVries, 2009).While, phylogenteic history shows that butterflies have affinity to the tropical environment, evolution of cold tolerance in the new derived taxa allows them to colonize colder climatic regimes (DeVries, 2000; Hawkins & DeVries, 2009). This phenomena plausibly explains the vertical colonization of beetle in the Southern Brazil (Lobo &Halffter, 2000; daSilva, 2018 a,b). The Palearctic fauna that diversified in colder Turkmenian and Mediterranean sub regions probably colonized the west of Himalaya in the Pleistocene when the mountains have been lifted (at least above timberline). These species later radiated while moving eastward through high elevation passes. The colonization history of butterflies suggests that historical dispersal mechanism shaped the current assemblages of butterflies in the Himalayan landscape.

4.5 Conclusion

High beta diversity of butterflies were recorded in this study. Beta diversity peaked at mid elevation coinciding with vegetation transition zones. Turnover (incidence based) or balanced variation (abundance based) components of beta diversity contributed mostly to the overall dissimilarity indicating that assemblages of butterflies were unique at each elevational zone along the gradient. The resultant pattern of beta diversity is largely due to environmental filtering rather than geographic extent. The analysis of suggest that niche division among species is primarily due to the affinities of butterflies to different biogeographical realms. The current assemblage of butterflies in the Himalaya can be linked to the colonization history. More empirical studies on phylogeography of butterflies covering many elevation gradients across the Himalaya is necessary in order to understand the colonization history and current assembly of butterflies in the Himalaya.

CHAPTER 5

RANGE SIZE DISTRIBUTION, RAPOPORT'S RULE AND DENSITY-RANGE SIZE RELATIONSHIP

5.1 Introduction

The large variation in distributional range size of organism is perhaps one of the most remarkable features of the living world (Gaston, 1996). The range size distribution shows distinct bio-geographical patterns and is often associated with ecological requirements and evolutionary history of an organism (Kreft et al., 2010). The information on range size provides an important input in delineating distribution pattern of biotic community. Additionally, such empirical studies would be crucial in order to delineate the effect of climate change on species with various range sizes. Vulnerability of a species is linked to range size of their distribution, for example, small-range species are generally more threatened by climate change than large-range species. Hence, information on range size profile of species is crucial in formulating conservation strategyfor the protection of more vulnerable species (Grenyer et al., 2006).

Several hypotheses has been purposed to explain the range-size patterns along different geographical gradients, among which Rapoport's rule is mostly discussed by the ecologists and biogeographers(Rapoport, 1982; Stevens, 1989).Rapoport's rule proposes that the latitudinal range size of species decrease from pole towards the tropics. The species on the higher latitude are able to withstand higher climatic regime and, hence, has a wider latitudinal range, whereas species at lower latitudes experiences more or less uniform climatic conditions and are unable to tolerate fluctuations in climate parameters (Stevens, 1989; Addo-Bediako et al., 2000). The latitudinal Rapoport's rule has been widely examined by various biogeographers around the globe and is considered as one of the important explanations for declining species diversity of various taxa from equator to poles (Colwell & Hurt, 1994; Šizlinget al., 2009; Luo et al., 2011). The concept was later extended to explain biogeographic patterns along the elevational gradients (Stevens, 1992). According to Rapoport's elevational rule, ranges of plants and animals increases with increasing elevation i.e. high elevation species has larger range sizes compared to low elevation counterparts. The increase in climatic variability with elevation was proposed to be potential mechanism for Rapoport's rule (Stevens, 1989,1992).Thus, species in the high elevation experiencing higher climatic variability would require adaptation that would lead them to occupy larger ranges. It has been advocated that Rapoport's rule is applicable mostly to larger geographical extent such as latitudinal gradient, whereas it has little or no support at smaller geographical scales such as elevation gradient (Dunn et al., 2007) but there are some exceptions (Fleishman, 1998; Sanders, 2002;Chatzaki et al., 2005). Hence, it necessitates to undertake empirical studies involving different taxa in various mountains to understand the applicability of Rapoport's rule in distribution of organisms.One of the important aspects in biogeography where Rapoport's rule have been used is to link the decrease in species richness with increasing range-size along the gradients corresponding with climatic variability and source-sink dynamics (Janzen, 1967; Stevens, 1989, 1992). Accordingly, range size and richness assumes a negative linear relationshipwherein species range size increases while the richness decreases along the elevational gradients.This assumption would be nullified if (i)range size shows mid elevational peaks or decreasing trend and (ii) richness trend peaks at mid elevation or shows increasing trend along the elevation (McCain &Knight, 2013). The species richness of butterflies follows a linear declining trend along the elevation in the Rangeet valley. However, whether butterfly community follow positive elevation-range size relationship as per Rapoport's rule still remains to be tested and validated.

The positive correlation between the abundance or density of species and range size is also one of the intriguing observed spatial variations (Brown, 1984). According to Brown (1984), the species having large range size tend to be more abundant throughout their distributional range while species with small range usually have comparatively low abundance. This relationship was later supported by many studies and was termed as population density-range size relationship or rule (Gaston et al., 1997; Lawton, 1993; Pimm & Jenkins, 2010). The plausible explanation for sucha pattern is that the species with larger ranges have less specialized niche requirements and, hence, able to adapt to wide range of habitats and expand their population. In contrast,small-range species are more specialized to a certain niche and are comparatively rare. Over the years, the positive relationship between density and range size has received support for many taxa ina spectrum of spatial scales (Russell & Lindberg, 1988; Macpherson, 1989; Verberk, et al., 2010).The positive relationship between density and range size relationship is now considered as a universal phenomenon or a global ecological rule (Gaston & Lawton, 1990; Pimm & Jenkins, 2010). However, some studies have also found negative density-range size relationships or no relationship as well (Gaston, 1996; Komonen et al., 2009; Pianka, 2014).

In the Rangeet Valley, the overall density of butterfly community decreases linearly with increasing elevation (Chapter 3). The observed decreasing trend in density is mainly due to the representation of more species that are rare and with small-range sizes. Majority of the small-range species are highly specialized to atropical climate (with higher Actual Evapotranspiration) and complex vegetation structure. Thus with changing environmental conditions along the elevation, population of small-range species also decreases rapidly. Butterfly community in the study areaalso constitutes species that are able to withstand larger climatic regimes. These species have comparatively large range size and occupy large elevational extent of the mountains. Hence, it is evident to predict that the population density of large range butterflies may show a distinct pattern along the elevational range of their occurrence.It has been proposed that species are more abundant in and around the midpoint of their distribution range and declines near the boundaries(Bock &Ricklefs, 1983). Brown (1995) supported this theory and predicted that the pattern can be found in an array of spatial extent ranging from local steep environmental gradients to the entire geographic range of species occurrence. The centered abundance pattern has been demonstrated only for plants in the montane ranges (Whittaker 1956, 1960, 1967; Whittaker &Niering, 1965). Based on this theory, here I hypothesize that the abundance of the large-range butterfly species peak at middle of their total elevational distribution range.

With this background, I analyzed the elevational range size and evaluated the applicability of Rapoport rule in butterfly community of the Rangeet Valley. The range size distribution is taxon specific and is related to difference in eco-physiological traits of the organisms. Traits such as biogeography affinity, phylogenetic relatedness and diet–breadth of different taxa have been shown to influence range-size distribution of organisms(Oommen& Shanker, 2005; Zhou et al., 2019). Thus,I also investigated the range size pattern of different groups of butterflies categorized according to the family, biogeographic affinity and larval host plant specificity. I tested whether the range-size distribution varies within these groups. I also examined thedensity-range size hypothesis in butterfly community of Rangeet Valley. I then assessed the density pattern of large range butterflies along the elevation to examine if the large range species are more abundant atthe middle elevation. Since density can be affected by environmental or spatial factors, I assessed the effect of different predictor variables on density pattern of large range-butterfly species in the Rangeet Valley.

5.2 Methodology

5.2.1 Butterfly sampling and data collection/collation on predictor variables

The present study was conducted in Rangeet Valley, Sikkim, Eastern Himalaya (details of the study area are provided in Chapter 2). Butterflies were sampled following fixed width point count methodcovering theelevation range of 300-3000m. Data on predictor variables such as tree species richness, tree density, shrub richness, shrub density, AET, NDVI and area were derived using primary sampling and secondary sources (details ,ore details is provided in Chapter 3).

5.2.2 Data Analysis

Range size was assigned to the entire butterfly species recorded during the study following the methodology of Stevens (1992). The elevational range of the species was considered as the difference between lowest and the highest elevations from where the species was recorded. Some species were recorded at only one site, hence, 100 meters was added to the elevational range of each of the species (±50 m at the highest and lowest elevation range). Species recorded at only one elevational site can be arbitrarily considered to have approximately 100 meter elevational range. The range size may vary between different ecological groups within same taxa depending on climatic adaptation and eco-physiological traits (Oommen& Shanker, 2005; Zhou et al., 2019). Therefore, using Kruskal-Wallis H test (owning to non-normality of the dataset), I first tested if there were any significant variation in range size between different groups of butterflies categorized according to (i) family, (ii) biogeographic affinity and (iii) larva host pant specificity (details of the categorization method is provided in Chapter 3). In order to test the elevational Rapoport's rule, I calculated the mean elevational range of overall butterflies community in each elevation and that of different sub-groups within a group. I then used ordinary least squares regression with linear models to analyze the range size pattern of overall butterflies and different groups along the elevation. All the analysis were conducted in R software (version 3.6.3)

In order to examine the density-range size relationship, Iseparately estimated abundance of all the 253 species of butterflies encountered during the study. The total abundance was considered as a sum of total number of individuals of a species encountered in each elevation. Since abundance data are subjected to variation due to unequal sampling, abundances of each species were converted to density (per hectare) following Reynolds et al. (1980(details provided in Chapter 3). In order to test the relationship between density and range size of each species, ordinary least squared regression using linear models was used. I also examined the pattern of population density of the large-range species and tested the centered abundance hypothesis for these species. For this purpose, ten species from different families, that had the largest elevational range in the Rangeet Valley were selected.The range size of these species were more than half of the elevational extent (>1500m) of the gradient considered in this study. The species selected were Painted Lady (*Vanessa cardui*),Pea Blue (*Lampides boeticus*), Red Helen (*Papilio helenus*), Striped Blue Crow (*Euploea mulciber*), Indian Tortoiseshell (*Agliascaschmirensis*), Indian Red Admiral (*Vanessa indica*), Straight Banded Treebrown (*Lethe verma*), Dark Judy (*Abisarafylla*), Indian Cabbage White(*Pieris canidia*)and Yellow Spot Swift (*Polytremiseltola*). The relationship between population density of large-range species and elevation was tested using both linear and quadratic models. For linear regression models, only elevation was used as a predictor variable, while for quadratic regression models elevation and elevation^2 was used as a predictors. The linear and quadratic models were compared using Akaike Information Criteriion(AIC). The model with lowest AIC was considered as the best fit to explain the density pattern of large-range species along the elevation. To assess the effect of spatial and environmental variables on population density I used generalized linear models (GLMs) with poisson distribution error (more details is provided in Chapter 3).A total of 128 GLMs were generated using the package *glmulti* (Calcagno & de Mazancourt, 2010)in Rsoftware (version

3.4.3).Among these models, the top explanatory model was considered to be the one with the lowest AIC_c. Models with $AIC_c < 2$ than the top ranked model is also considered equally likely to explain the variation in density of large-range butterfly species (Burnham & Anderson, 2002) All the models contain different set of predictor variables, therefore, the likely models were averaged in order to assess the relative importance of the individual parameter in the models.

5.3 Results

5.3.1 Range size distribution along the elevational gradient

The elevational range size of butterflies varied from 100m to 2850m in the Rangeet Valley. Majority of the butterflies recorded in the study area had narrow elevational range (**Figure5.1**). Analysis of the range size of all the butterflies (irrespective of their elevational distribution) shows that 90.11 % had range size lesser than 1500 m while only 9.09 % of had range size greater than 1500 m (half of the total elevational stretch considered during the study). Among the small range butterflies, approximately 40 % were restricted to single elevation zone.

The mean range size of different butterfly families differed significantly (**Figure 5.2**). Nymphalidae had the highest mean elevational range size followed by Papilionidae, Riodinidae, Pieridae, Lycaenidae and Hesperiidae (Kruskal-Wallis chi-squared = 11.280, df = 5, $p \leq 0.05$). Amongst the butterflies with different biogeographic affinity, Palearctic species had significantly higher range size, followed by global and oriental species (Kruskal-Wallis chi-squared = 15.229, df = 5, $p \leq 0.05$). The range size of butterflies of different feeding guild (larval host plant specialization), however, did not show any significant differences.

The mean elevational range of overall butterfly community increased significantly with the elevation (**Figure 5.3**). The increase in range size with elevation indicates that most of the narrow ranged butterflies were restricted to low elevation (**Table 5.1**). However, at sub-group levels, range size-elevation relation showed marked variation. Species belonging toNymphalidae, Papilionidae, Lycaenidae, Oriental, global, oligophagous and polyphagous sub-groups showed a declining trend with elevation, whereas range-size of Pieridae, Hesperiidae, Riodinidae, Palearctic and Monophagous species did not fit to a linear declining model.

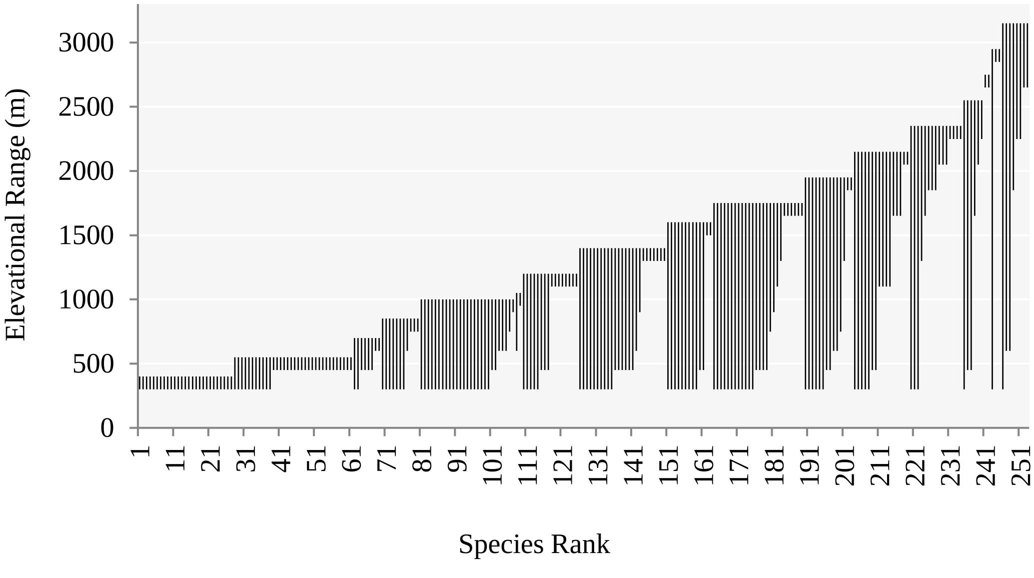


Figure 5.1: Elevational range profiles of butterflies in Rangeet Valley Sikkim, Eastern Himalaya. Vertical bars indicate Upper and Lower elevational limits of butterflies (the species rank are according to serial numbers given for species in Table A3.1).

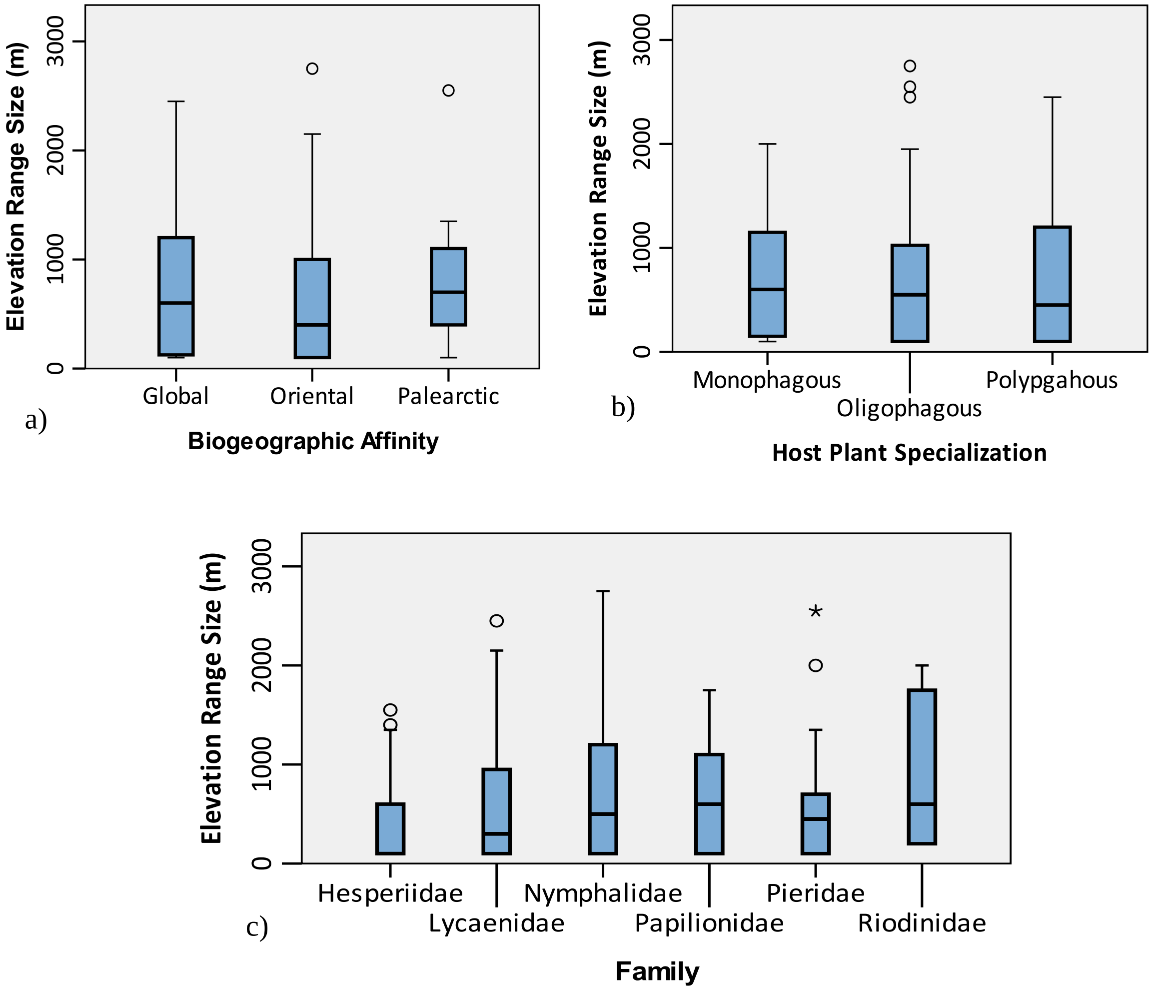


Figure 5.2: Comparison of elevational range size of different groups of butterflies observed in the Eastern Himalaya; (a) Biogeographic affinities (b) Host plant specializations(c) Families.

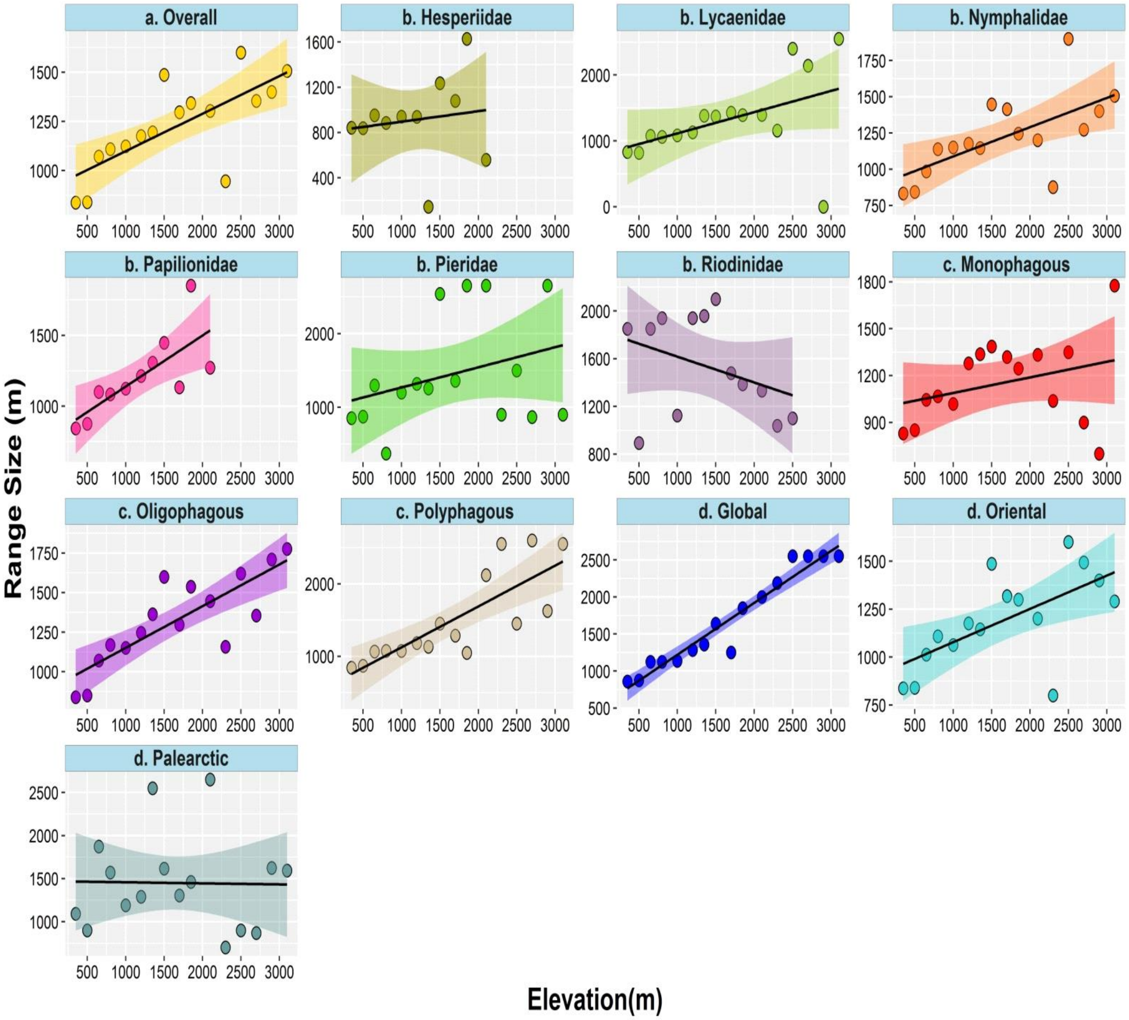


Figure 5.3: Mean elevational range of overall and different groups of butterflies along the elevation in Rangeet Valley, Sikkim, Eastern Himalaya ; (a) Overall, (b) family, (c) feeding guild and (d) biogeographic affinity

Table 5.1: Ordinary Least squared regression of elevational range size of butterflies (total as well as different sub-groups)with elevation in Rangeet Valley, Sikkim, Eastern Himalaya.

Butterfly groups	**Coefficient**	**Std.Er**	**R^2**	**t - value**	**Pr(>|t|)**
Total	2.816	0.698	0.538	4.037	**0.001****
Nymphalidae	2.036	0.651	0.411	3.127	**0.007****
Papilionidae	1.555	0.459	0.560	3.386	**0.008****
Hesperiidae	0.224	0.512	0.020	0.437	0.672
Lyacenidae	1.383	0.213	0.764	6.482	**0.001****
Riodinidae	-0.600	0.468	0.130	-1.282	0.226
Pieridae	0.376	0.297	0.103	1.266	0.226
Global	1.335	0.094	0.935	14.225	**0.000****
Palearctic	-0.031	0.422	0.000	-0.073	0.943
Oriental	2.279	0.752	0.396	3.031	**0.009****
Monophagous	1.043	0.818	0.104	1.275	0.223
Oligophagous	2.575	0.474	0.678	5.430	**0.001****
Polyphagous	1.155	0.226	0.651	5.113	**0.001****

Coefficient of regression, standard error (Std. Error), R^2 representing the proportion of variance of regression, and t-value along with overall significance of the regression are presented. ** Significant at $p < 0.01$, Negative relationships are indicated by minus (-) sign. Significant p-values are highlighted as bold font

5.3.2 Density-Range size relationship and density pattern of large-range species

Abundances of butterflies varied from single detections of around 52 species to 170 individuals (4.72% of the total individuals) of the most commonly observed Three-spot Grass Yellow (*Eurema blanda)*. Red Helen (*Papilio helenus)* representing about 3.58% individuals (129 butterflies), Chocolate Pansy (*Juninio iphita*) with 2.91%individuals(105), Yellow Orange Tip (*Ixias pyrene)* with 2.86% individuals (103) and Glassy Tiger (*Parantica aglea*) with 2.83 % individuals (102) were other notable common species in the study area. The total density of butterfly species on an average were positively correlated with their elevational range size (R^2= 0.231, p< 0.001) (**Figure 5.4**).

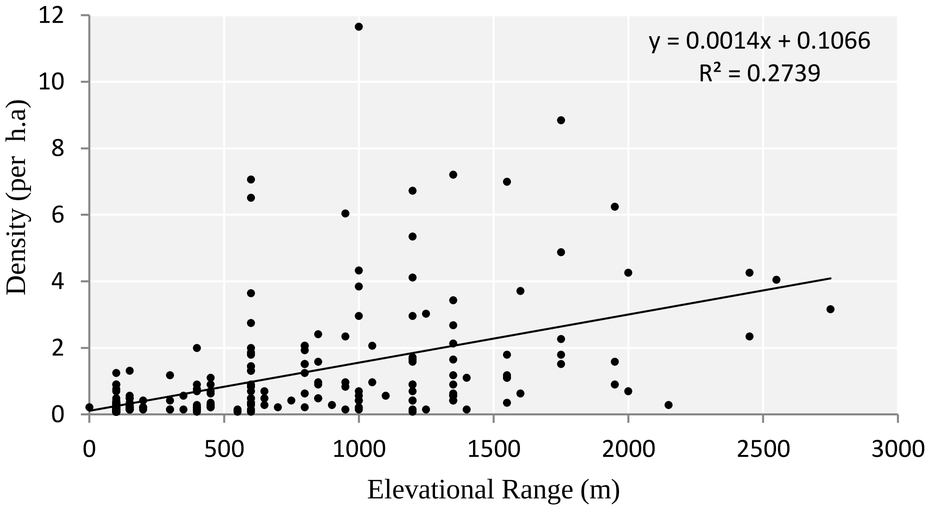


Figure 5.4: Relationship between density and elevational range size of butterflies (*n=253*) in the Rangeet Valley, Sikkim, Eastern Himalaya.

Among all the butterflies observed during the study, 10 species had the most large-range size as compared to other species. (**Table A.1; Figure 5.5**). The density of different large-range species showed varied pattern along the elevation (**Table 5.2; Figure 5.6, 5.7**). The linear model performed best for species such as Painted Lady (*Vanessa cardui),* Pea Blue (*Lampides boeticus*), Red Helen (*Papilio helenus*) and Striped Blue Crow (*Euploea mulciber*). Density pattern of Painted Lady (R^2= 0.534, $p<0.01$)and Pea Blue(R^2 = 0.428, $p<0.01$) showed increasing trend while density ofRed Helen(R^2 = 0.578, $p<0.01$)and Striped Blue Crow(R^2= 0.758, $p<0.01$)followed decreasing trend with elevation.Quadratic models best explained the variation observed in density pattern of Indian Tortoiseshell (*Aglias caschmirensis*)(R^2= 0.768, $p<0.01$), Indian Red Admiral (*Vanessa indica*) (R^2=0.475, $p< 0.05$), Straight Banded Treebrown (*Lethe verma*)(R^2= 0.460, $p<0.05$)and Dark Judy (*Abisara fylla*)(R^2= 0.642, $p<0.01$). Density pattern of Indian Tortoiseshell decreased gradually from the lower elevation to middle elevation and then increased significantly in the higher elevation. Population density of Indian Red Admiral showed a negative hump with lowest density recorded in the middle elevation. The density of Straight Banded Treebrown and Dark Judy showed a mid-hump with highest density at the middle elevation. The density pattern of Indian Cabbage White (*Pieris canidia)* and Yellow Spot Swift (*Polytremis eltola*) did not show any significant trend along the elevation gradient.

Different sets of GLM models explained the density pattern of each of the large range species of butterflies (**Table 5.3**). Averaged model sets showedthat the density of Straight Banded Treebrown was positively correlated with AET, tree species richness and area.Pea Blue showed negative relationship with AETand area and a positive association with shrubs richness and density. The density of Red Helen showed positive relationship with AET and tree density. Similarly, Yellow spot swift revealedpositive relationship with tree density. Striped Blue Crow (*Eupolea mulciber*) showed positive association with AET and spatial area. The density of Dark Judy was best explained by tree species richness and area. Density pattern of Indian Tortoiseshell, Indian Cabbage White, Indian Red Admiraland Painted Lady did not show any significant relationship with any of the predictor variables considered here.

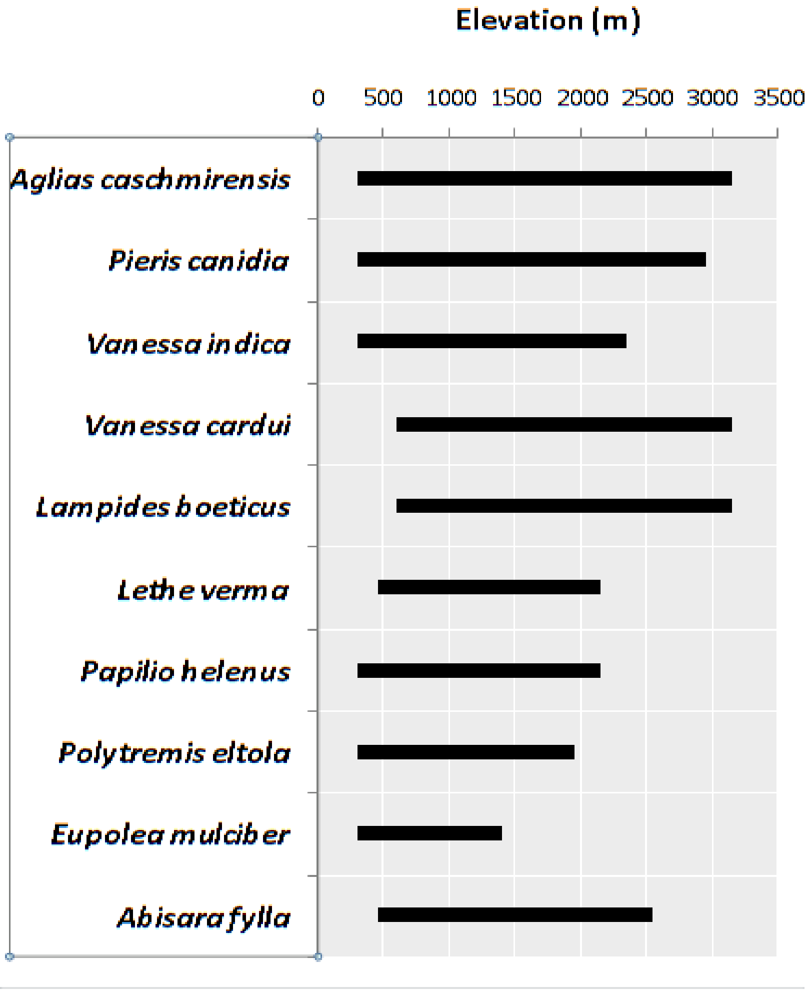


Figure 5.5: Elevational range profiles of large range butterflies observed in the Rangeet Valley during the study.

Table 5.2: Ordinary least squared regression (linear and quadratic) models showing the relationship between population density of large-range species of butterflies and elevation observed in the Rangeet Valley, Eastern Himalaya.

Common Name	**Scientific Name**	**Regression Models**	$\mathbf{R^2}$	**Pr(>|t|**	**AIC**
Indian Tortoiseshell	*Aglias cashmirensis*	$\sim 0.0033\ \text{Elevation}\ -2.405$	0.466	0.003**	87.434
		$\sim -3.641^{-06}\ \text{Elevation}^2\ -9.045-^{03}\ \text{Elevation} + 5.475$	0.768	<0.001***	76.084
Indian Cabbage White	*Pieris canidia*	$\sim -0.0006\text{Elevation} + 5.5713$	0.05561	0.417	87.434
		$\sim -2.252^{-06}\ (\text{levation})^2 + 6.613-^{03}\text{Elevation} + 1.182$	0.3951	0.06302	76.084
Red Admiral	*Vanessa indica*	$\sim -0.001\text{Elevation}\ -4.642$	0.282	0.0342*	82.530
		$\sim 2.153-^{06}\ \text{Elevation}^2 - 9.271-^{03}\ \text{Elevation} + 9.303$	0.4752	0.0151*	79.518
Painted Lady	*Vanessa cardui*	$\sim 0.002\ \text{Elevation}\ -1.853$	0.534	<0.001***	74.119
		$\sim 4.273-^{04}\ \text{Elevation}^2 + 4.273-^{04}\text{Elevation} - 0.5117$	0.5515	0.005**	75.504
Pea Blue	*Lampides boeticus*	$\sim 0.0042\ \text{Elevation}\ -2.756$	0.4284	0.005**	97.23
		$\sim 5.471-^{07}\ (\text{Elevation})^2 + 2.367-^{03}\text{Elevation} - 1.572$	0.432	0.025*	99.127
Straight Banded	*Lethe verma*	$\sim -0.001\ \text{Elevation} + 6.599$	0.1014	0.229	97.311

Treebrown		$\sim -4.164e^{-06} (\text{Elevation})^{2} + 1.254^{-02}\text{Elevation} - 2.414$	0.4602	0.018*	91.1577
Red Helen	*Pailio helenus*	$\sim -0.008\ \text{Elevation} - 22.541$	0.578	<0.001***	109.49
		$\sim 2.116^{-06} (\text{Elevation})^{2} - 1.561^{-02}\ \text{Elevation} - 27.12$	0.599	0.002**	110.71
Yellow Spot Swift	*Polytremis eltola*	$\sim -0.001\ \text{Elevation} - 2.127$	0.068	0.327	74.098
		$\sim 5.226^{-05} (\text{Elevation})^{2} - 6.109^{-04}\ \text{Elevation} - 1.366$	0.0695	0.626	76.080
Striped Blue Crow	*Eupolea mulciber*	$\sim -0.0048\ \text{Elevation} - 12.989$	0.7589	<0.001***	78.919
		$\sim 1.290^{-06} (\text{Elevation})^{2} - 9.293^{-03}\text{Elevation} - 1.578^{+01}$	0.788	<0.001***	78.972
Dark Judy	*Abisara fylla*	$\sim 3.7673\ \text{Elevation} - 0.001$	0.0048	0.798	96.148
		$\sim -5.087^{-06} (\text{Elevation})^{2} - 1.766^{-02}\ \text{Elevation} - 1.578$	0.6423	0.002**	81.7757

Coefficient of regression, R2 representing the proportion of variance of regression, and AIC along with overall significance of the regression are presented. ***Significant at p < 0.001, ** significant at p <0.01, Negative relationships are indicated by minus (-) sign. Significant relationships are highlighted as bold font.

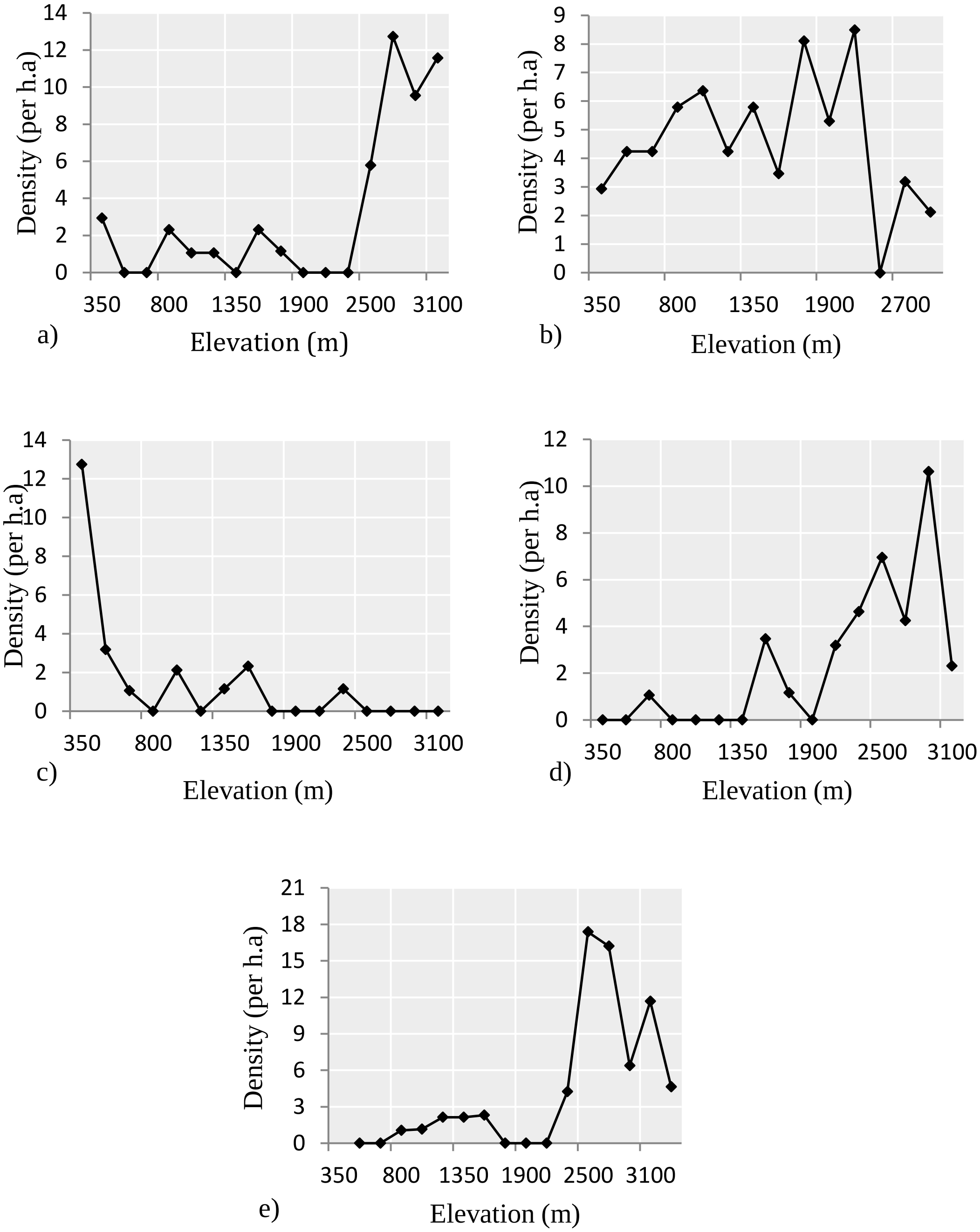


Figure 5.6: Population density pattern of select large range butterfly species along the elevational gradient in Rangeet Valley; a)Indian Tortoiseshell (*Agliascaschmirensis*), b) Indian Cabbage White *(Pieris canidia*),c)IndianRed Admiral (*Vanessa indica*), d) Painted Lady (*Vanessa cardui*), e) Pea Blue(*Lampidesboeticus*).

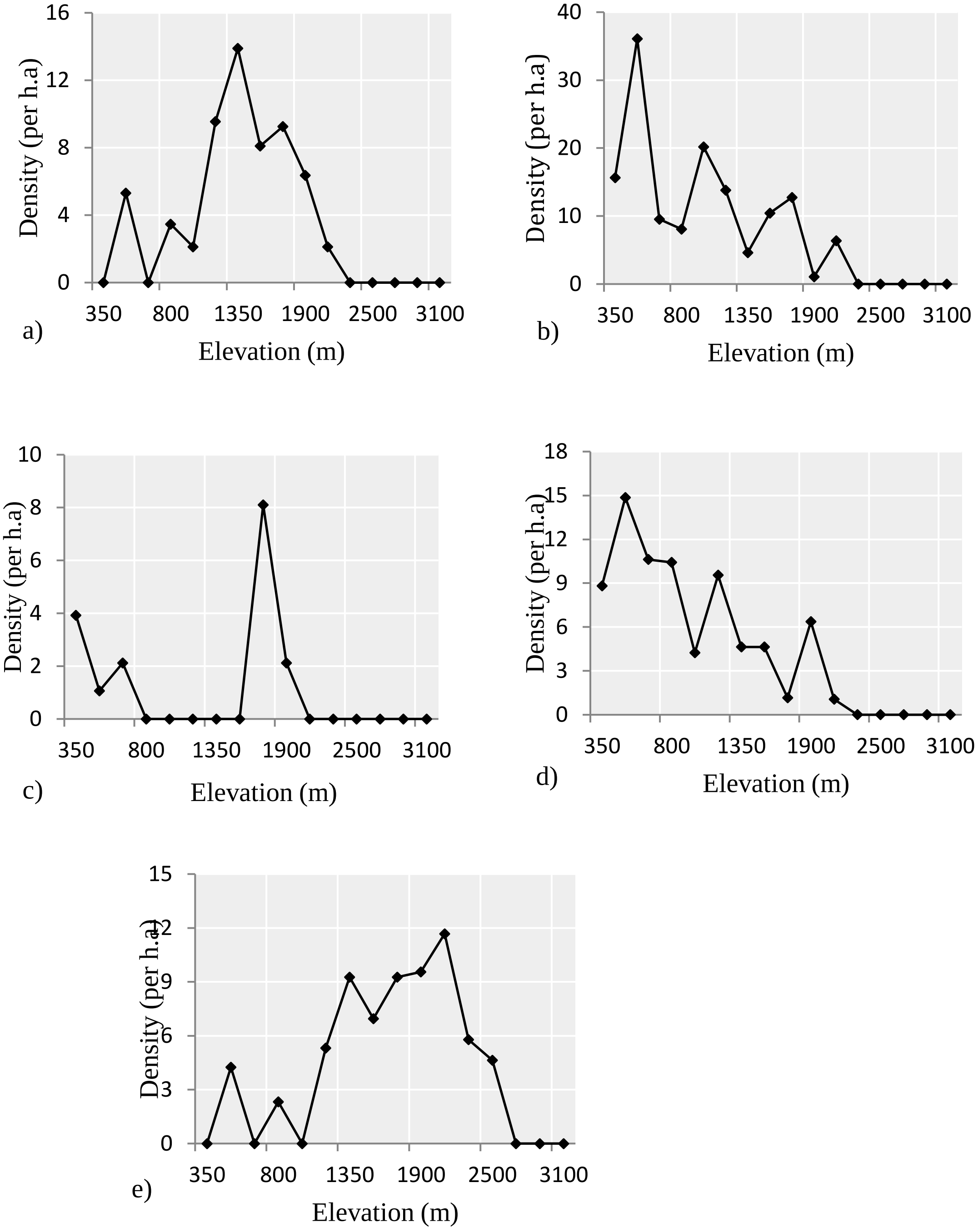


Figure 5.7: Population density pattern of select large range butterfly species alongthe elevational gradient in Rangeet Valley; (a) Straight Banded Treebrown (*Lethe verma*), (b) Red Helen (*Papiliohelenus*),(c)Yellow Spot swift (*Polytremis eltola*), (d) Striped Blue Crow (*Eupolea core*), (e)Dark Judy (*Abisara fylla*).

Table 5.3: Summary of model averaged estimates (GLM) of predictor variable in explaining variation in density (numbers per h.a) of large-range butterflies along the elevation gradient in Sikkim, Eastern Himalaya using the multimodal inference.

Common Name	**Scientific Name**	**AET**	**TSR**	**TSD**	**SSR**	**SSD**	**NDVI**	**Area**
Indian Tortoiseshell	*Agliascaschmirensis*	-	-	-	-	-	-	-
Indian Cabbage White	*Pieris canidia*	-	-	-	-	-	-	-
Red Admiral	*Vanessa indica*	-	-	-	-	-	-	-
Painted Lady	*Vanessa cardui*	-	-	-	-	-	-	-
Pea Blue	*Lampidesboeticus*	**-0.007****	-	-	**0.103****	**0.020****	**12.869****	**-0.038****
Straight Banded Treebrown	*Lethe verma*	**0.008 ****	**0.122 ****	-	-	-	-	**0.016****
Red Helen	*Polytremiseltola*	-	-	**0.027****	-	-	-	-
Yellow Spot Swift	*Papiliohelenus*	**0.126****	-	-	-	**0.001 ****	-	-
Striped Blue Crow	*Eupoleamulciber*	**0.010****	-	-	-	-	-	**0.007****
Dark Judy	*Abisarafylla*	-	**0.084****	-	-	-	-	**0.010****

The numbers represents estimates of predictor variables. ** Significance at $p < 0.01$. "–" indicates doesnot show any association. Actual Evapotranspiration (AET), Tree Species Richness (TRS), Tree Density (TRD), Shrub Species Richness (SSR), Shrub Density (SSD), Normalized difference vegetation index (NDVI)

5.4 Discussion

5.4.1 Range size distribution and test for Rapoport's rule

Majority of butterflies had a narrow elevational range in the Rangeet valley while relatively few species had large elevational range. Similar trends in elevational range size distribution of butterflies have been demonstrated by other studies as well (Flieshman, 1998; Pyrcz et al., 2009; Acharya & Vijayan, 2015). Narrow range size of majority of butterflies indicates that relatively large proportion of butterflies are sensitive to environmental changes and are, thus,affected by climate (Levanoni et al., 2011). Environmental tolerance, habitat specificity and dispersal capability, and physiology are known to influence elevational range size of organisms (Levanoni et al., 2011). Most of the large range species belonged to family Nymphalidae and Papilionidae. Butterflies of Nymphalidae and Papilionidae family are known to have higher dispersal capability than members of other butterfly family and, hence, adapt to wide range of environmental regimes (Dennis et al., 1995). It is due to the representation of such species that the mean range size of Nymphalidae and Papilionidae was higher than other families such as Hesperiidae. Further, it has been well established that body size directly correlates with the dispersal capability and, hence, the range size of the insects (Kuussaari et al., 2014). The members of the families Nymphalidae (average wing size = 65.20mm) and Papilionidae (average wing size = 111.41mm) have relatively larger wing size and, therefore, have larger dispersal capacity. Hesperiidae (40.68mm), Lycaenidae (33.41mm) and Pieridae (60.55mm) are represented by smaller butterflies having restricted dispersal capabilities resulting into smaller range sizes. There are evidences from the Himalayan plants that tropical species have smaller elevational ranges than the temperate or widely distributed species (Zhou et al., 2019; Li & Feng, 2015). This study also found higher average range size of Palearctic species compared to the Oriental or Global species. The palearctic species are the highland butterflies fauna that are adapted to tolerate broad range of climatic variability along the elevation and,therefore, able to colonize wide environmental gradients. Meanwhile the oriental and global species are mostly tropical species that are adapted to narrow climatic niches as a result of which they have smaller elevational rage size.

The mean elevational range of the butterflies increased with increasing elevation in accordance with the Rapoport's rule. Rapoport's rule explains that the range size of the species increases with the increasing latitude, because the climatic tolerance of the species in lower latitude is generally lower than that of species occurring in the higher latitude. The relationship of the elevation range and richness can be explained by Rapoport's rescue hypothesis (Stevens, 1992). The hypothesis explains that the species with smaller range are more restricted to the lower elevation as they are unable to tolerate the climatic condition of the higher elevation. The species of the higher elevation have larger elevational ranges because of their broad tolerance to climatic fluctuations. The colonization of species from higher elevation to the lower elevation leads to increase in the species in the lower elevation ultimately resulting in monotonic decline pattern of species richness. While Rapoport's rule along the elevation gradient has been tested for many taxa, its applicability remains much controversial (Colwell & Hurt, 1994). However, there are evidences on applicability in insect taxa such as ants (Sanders, 2002), moths (Brehm et al., 2007) and even butterflies (Fleishman, 1998).

5.4.2 Density-range Size relationship and density pattern of large-range species

The densities of butterflies were positively correlated with their elevational range-sizes as predicted by the density-range size rule. Along the global or regional scale, most studies found positive linear relationship of density-range size in different taxa such as plants (Brown,1984) molluscs (Russell & Lindberg, 1988), macro-invertebrates (Verberk et al., 2010) and birds (Novosolov, et al., 2017). Brown (1984) found significant positive relationships between elevational range size and abundance in North American plants and insects along elevational gradient. Gaston (2003) noted the decline in predictive power of abundance–range size relationship with increasing spatial grain size. Thus, at local gradients the density-range size may show a weaker relationship similar to the findings of McCain (2006) for rodents along a Caribbean elevational transects in Tilarian mountain range in Costa Rica. The spatial grain size (restricted to a local elevational gradient) of the present study area may perhaps be responsible for the weaker relationship between density and range size ($R^2= 0.231$, $p< 0.001$). Additionally, the presence of many species with lower abundances might have resulted into weak relationship between abundance and range size (McCain, 2006). Further, not all of the abundant species have larger range size, for example, abundant species such asThree Spot Grass Yellow (*Eurema blanda*), Chocolate Pansy (*Juninio iphita*), Yellow Orange Tip (*Ixias pyrene*) had small elevational range and mostly occurred in lower elevational areas. Thus, the perceived pattern may be related to taxa and scale of the study and may require further analysis with the inclusion of geographic range of butterflies in order to test the generality of density-range size relationship.

I analyzed the density pattern of ten wide ranging butterfly species along the elevational gradient. Straight Banded Treebrown (*Lethe verma)* and Dark Judy (*Abisara fylla*) exhibited a midelevation peak in densities. Other than mid elevational peak the other decreasing as well as increasing trend in density of large-range butterflies along the elevation was observed. The variation in the population structure of different species along the elevation reflects adaptation to different climatic regimes and specific life history strategies. Indian Red Admiral (*Vanessa cardui*), Indian Tortoiseshell (*Aglias caschmirensis*) and Pea Blue (*Lampides boeticus*) have widest range size amongst the Himalayan butterflies (Haribal, 1992; Kehimkar, 2016). Since only few species are able to tolerate the colder climate, higher elevational zones most probably provide larger niche space and resources as competition reduces due to decrease in overall butterfly diversity. On the other hand, species such Red Helen (*Papilio helenus*) and Striped Blue Crow (*Euploea mulciber*) represents tropical species that are most abundant in the lowland and have few individuals at mid elevation (their uppermost range extent). These species have narrow environmental tolerance as compared to the species such asIndian Red, Indian Tortoiseshell,and Pea Blue. Similar to our findings, McCain (2006) showed mixed pattern of abundance among Costa Rican rodents along the elevation with only one rodent species showing a mid-elevational hump. Therefore, our findings suggest that centered abundances (Brown, 1995) may not be absolute for all the species along the elevation.

Large range species showed varied relationships with different environment and spatial variables. AET was among the most important variable that explained mush of the variation in population size of Straight Banded Treebrown, Red Helen and Striped Blue

Crow. AET also influenced the overall richness, density and beta diversity pattern of butterflies in the Rangeet Valley (details provided in Chapter 3 and 4). Higher AET in the lower elevation is related to the availability of water and thermal energy that is essential in maintainingphysiology oftropical butterflies (Hawkins &Porter, 2003a). AET also functions indirectly by influencing the productivity of the ecosystems (Fleishman et al., 2005). Tree species richness was significantly correlated to the density pattern of the Straight Banded Treebrown and Dark Judy.The peak density of these species observed at mid-elevation corresponds to mid-elevational peak observed in tree richness in the Eastern Himalaya (Acharya et al., 2011a; Rana et al., 2019). Straight Banded Treebrown and Dark Judy are exclusively found in the forested areas, hence, well preserved forest in the mid elevation act as important refuge for maintaining their population. Tree density was found to be strong determinant of population size of Yellow Spot Swift (*Polytremiseltola*) which represents another forest species. On the other hand, population of species such as Pea Blue (which is mostly found in open land) (Kehimkar, 2008) was affected by density and richness ofshrubs. Since Pea Bluedepend on various shrub speciesbelonging to family Fabaceae (Haribal, 1992; Kunte et al., 2019), open habitat that favors growth of these shrubs is important for their life cycle. Density of Indian Tortoiseshell, Indian Cabbage White, Indian Red Admiral and Painted Lady did not show any significant relationship with any predictor variables considered during the study. Hence, other drivers of butterfly population such as distribution pattern of host plants, nectar plants, and specific ecological requirements of the species should be explored to understand the density pattern of butterflies along the elevation in mountains.

5.5 Conclusion

In general, I observed that majority of the butterflies had narrow elevational range with some species restricted to single elevational zone indicating that most of the butterflies in Rangeet Valley were sensitive to changes in environmental condition. The mean elevational range of the butterflies increased with elevation providing strong evidence for Rapport's rule.Moreover, range size also significantly varied among species in different butterfly families and biogeographic affinity. This indicates that the different groups within the same taxa may respond differentially to climatic changes and anthropogenic pressures.

The density of butterflies showed positive relationship with the elevational range size. However, the relationship was weak becausesomeof the most abundant species did not have large range. The density pattern of the large range butterflies also showed varied trend along the elevation indicating that even large range species may be affected by elevation and its associated factors in different ways.

CHAPTER 6

PHYLOGENY AND BIOGEOGRAPHY OF GENUS *Lethe* (NYMPHALIDAE: SATYRINAE)

6.1 Introduction

There is a little doubt that distribution of living organisms is determined by their ecology (McCain & Grytnes, 2010). Based on this foundation, most of the present day approach has focused to link the diversity pattern of a given group to the environmental factors. Even though the environment acts as a filter of species diversity, they themselves cannot increase or decrease diversity of an ecological community (Wiens & Donoghue, 2004). The historical biogeography seeks to understand “how” and “when” species or taxa assembled in said environments by integrating evolutionary history (speciation, dispersal and extinction) of an organism (Gutierrez, 1997; Wiens & Donoghue, 2004). The incorporation of historical biogeography in addition to ecological hypotheses has provided an evolutionary perspective in explaining the diversity gradients in the mountains (Willmott et al., 2001; Hall, 2005; Gillespie et al., 2013).

“Tropical niche conservatism” is one of the robust biogeographic hypotheses that have frequently been used to explain diversity along the spatial gradient (Wiens & Donoghue, 2004). The hypothesis is based on a founding principle that taxa having high tropical species richness originated in the tropics and have radiated to the temperate areas only recently. Since the tropical areas represent the ancestral niches, there is more number of species because of longer time available for speciation. Within the tropical clades, only few evolved to tolerate colder climates and thus radiated to new temperate climates. The tendency of majority of the species to retain their ancestral niches has helped in maintaining the disparity observed in species richness pattern. In the mountain region, the lowland tropical areas acts as a species “museum” where older clades accumulate while the higher elevation acts as species “pump” (Hall, 2005). The new clades possibly radiates to the higher elevation as a result of “vertical speciation” mechanism (Willmott et al., 2001; Hall, 2005). Niche conservatism is considered as strong explanation of diversity gradients for plants (Jin et al., 2015), butterflies (Hall, 2005), frogs (Smith et al., 2007) and salamanders (Wiens et al., 2007) along the elevation.

The study of biogeographic hypothesis often relies on the deep understanding of phylogenetic history and systematics of an organism (Santos & Amorim, 2007). The traditional use of morphological systematics sometime results in taxonomic misidentification that may impede perceived biogeographic trend (Monge-Nájera, 2008). For instance, Gill et al. (2014) showed high discrepancy between morphological and molecular phylogeny based (DNA barcoding) elevational species richness pattern of rotifers. DNA barcoding significantly changed richness values of a site by increasing the number of 49 morphospecies by splitting into 69 species. The site with the highest morphospecies richness was at 2411 m elevation, whereas the site with the highest barcode-taxon richness was at 2388 m. The use of molecular markers (especially barcode gene cytochrome c oxidase subunit I, (*COI*) have significantly contributed in easy delimitation of many closely resembling species, which otherwise would have been considered as single species leading into under estimation of biodiversity of the region (Hebert et al., 2004).

The taxonomically important characters in butterflies such as genitalia and wing coloration typically often vary even between closely related species occurring in different as well as in same geographical region. However, the presence of individuals which possess characters intermediate between two closely related species such as *Potanthus* sp. (Kunte et al., 2019) causes problems in the identification of taxa and may compromise the generally accepted species concept (Gillespie et al., 2013). The ‘intermediates’ may be either cryptic species or a population of single species with natural variation which appears as clusters in a particular space. Splitting a widespread species which are thought to be same but actually represent different species, increases the perceived biological diversity of a region. Molecular taxonomy of butterflies using DNA barcode gene has received wider attention globally. For example, DNA barcoding of once thought single species of skipper butterfly *Astraptes fulgerator* (described in 1775) revealed that it was a complex of 10 species with sympatric distribution (Hebert et al., 2004). Similarly, Burns et al. (2008) found *Peichares philetes* (once considered single species) as a complex of four species. In Argentina, barcoding of 417 species of butterflies revealed 444 barcode clusters suggesting that the perceived diversity was comparatively higher (Lavinia et al., 2017). In addition to the barcode gene, mitochondrial cytochrome oxidase c subunit II (*COII*), NADH-ubiquinone oxidoreductase chain *1* (*ND1*) and nuclear genes wingless (*Wg*), elongation factor 1-alpha (*Ef1a*), tektin, triose phosphate isomerase (*Tpi*), etc. are frequently being used to generate a well-supported phylogenetic tree of butterflies (Nylin et al., 2001; Peña et al., 2006 ; de Silva et al., 2010).

The butterfly genus *Lethe* with about 140 species globally belongs to subfamily Satyrinae under family Nymphalidae. Morphologically, the upper part of these butterflies is brown with apical spots on the forewing and spots or ocelli on the hindwing. They also bear distinctive ocelli on the under parts of the wings. Due to the presence of cryptic taxa such as *L. nicetella* (which was re-discovered recently after 120 years during the present study; Dewan et al., 2018) with only minute differences with *L. sidonis*, the genus is taxonomically challenging. The genus was last revised by Lesse (1957) and many more species have been described since then (Lang & Liu, 2014; Lang & Duan, 2016; Huang et al., 2019). More empirical research is necessary to understand the diversity and relationship of the genus based on mitogenome and nuclear genes. Additionally, the species rich genera such as *Lethe* serve as model group to test various biogeographic hypotheses.

Hence, in this study, I evaluated the phylogeny of genus *Lethe* and delineated the evolutionary relationship of the group. I also determined the time of origin and estimated the time of divergence of some species and clades under the genus. Finally, based on phylogeny and time of divergence, I explain the biogeography of the genus and their colonization in the Himalaya.

6.2 Methodology

6.2.1 Study species

Lethe is the butterfly genus of the sub-family Satyrinae under the family Nymphalidae. The genus was first described by Jacob Huber in the year 1819. The genus consists of about 140 species distributed across the oriental realm from Borneo, Sunda Islands, Japan, Siberia, Himalaya and peninsular India and Sri Lanka (Haribal, 1992). *Lethe* butterflies typically feed on various species of bamboo (Poaceae family) and occur in well forested regions. The key description of this genus provided by Marshall and de Nicéville (1882) is outlined below:

(i) Head is rather small and tufted, scarcely in front. Eyes are hairy and prominent, especially in the males. Labial palps is elongated, elevated obliquely as high as, or higher than the level of the top of the eyes, and extended to a short distance in front of the face. Antennae are scarcely, half the length of the forewing and consist of slender gradually formed club at the end which is composed of very short joints. Thorax is very short, thick, and hairy. Abdomen is small.

(ii) Forewing triangular or ovate with costal margin strongly curved towards the apex. The termen is straight, concave or oblique and the dorsum slightly convex or straight. Cell is not quite half the length of the wing. Discal cells rather variable, upper two sometimes oblique, when the upper apex of the cell becomes rounded. Veins 10 and 12 starts slightly before the apex of the cell. Vein 12 is slightly swollen at the base. The forewing usually consists of ocelli.

(iii) The Hind wing is mostly oval. The termen of the hindwing is strongly arched and often caudate at apex of vein 4. The cell is half the length of the wing. Discal cells are oblique. The vein 3 starts from the apex or before the apex. The hindwing consist of equal sized or variable ocelli.

In India, the genus *Lethe* is represented by 46 species (Varshney & Smetacek, 2015) of which the highest number of this species exist in the north-eastern region of India (Kehimkar, 2016). Two species, *Lethe rohria* and *Lethe europa*, are found throughout India. Sikkim Himalayan region consist of about 33 species of the genus (Haribal, 1992). The genus occupies well forested habitat at within the elevation of 300-3000m in the Sikkim Himalaya. Majority of the members of the genus occurs in the lowland tropical areas while few inhabit the higher elevation. Several biogeographic hypotheses can be tested by studying this diverse genus, as they represent a monophyletic group with many mountain and lowland species occurring in the same region.

6.2.2. Sampling and collection of butterfly samples

With a due permission from the Department of Forest, Environment & Wildlife Management, Government of Sikkim (Permit No: 78/GOS/FEWMD/BD-R-2015/CCF (T&HQ) 297 and 78/GOS/FEWMD/BD-R-2015/CCF (T&HQ) 328), specimens of genus *Lethe* (Table 6.2) were collected from various sampling locations in the Rangeet Valley (details of study area is given in Chapter 2). Out of 33 species of genus reported from Sikkim, a total of 13 species were encountered and could be collected during the study (**Table 6.1**). Altogether two or three specimens of each species were collected from each sampling site using nylon swipe net. The captured specimen was killed by carefully pinching in the thorax. With the wing over its back, the collected butterflies were gently slipped in a triangular envelope. All the collected specimens were put in an air tight box and brought to the laboratory. The collected specimens were stored at -4^{o}C in refrigerator to prevent putrefaction. Specimens were preserved following the standard protocol of

Table 6.1: Key morphological characters and elevational range size of *Lethe* spp recorded during the study. UP (upper part); UN (underneath); FW (Forewing); HW (Hindwing); UPF (Upper part forewing); UPH (Upper part hindwing);UNF (underneath forewing); UNH (underneath hindwing).

Sl. No	**Scientific Name**	**Common Name**	**Wingspan (based on specimen collected during the study)**	**Wingspan (based on literature)**	**Elevational Range Size in Rangeet Valley**	**Elevational Range Size (previous records)**	**Key identifying characters**
1.	*Lethe verma* (Kollar, 1844)	Straight Banded Treebrown	58-60 mm	55-60 mm	450-2150 m	500-3000 m	UP dark brown with large white discal band across FW.UNF two or three apical ocelli. UNH consists of five ocelli. Apical ocellus is the largest followed by second-last ocellus
2.	*Lethe confusa* (Aurivillius, 1898)	Banded Treebrown	60-61 mm	50-60 mm	300-1600 m	350-1700 m	Similar to *Lethe verma* but has white basal line across UN. The UNF has two black apical ocelli among which the first one is larger. UNH

							apical ocellus distinctively larger than the other ocelli.
3.	*Lethe kansa* (Moore, 1858)	Bamboo Forester	70 mm	65-75 mm	450-550 m	500-2000 m	UP pale brown and UN has a violet gloss. UNH ocellus in space 4 is out of line and forms a curve with other ocelli. The ocelli are surrounded by yellow ring.
4.	*Lethe sinorix*(Hewiston, 1863)	Tailed Red Forester	70-76 mm	75-77 mm	200-2160 m	450-2150 m	Similar to *Lethe kansa* but UPH more brownish. Two dark lines in the UN run parallel. HW poses a long tail which is reddish in colour. UHN ocellus in space 4is more out of line than the other ocellus.
5.	*Lethe latiaris* (Hewiston, 1862)	Pale Forester	60-62 mm	55-65 mm	900-1950 m	500-2400 m	UP brownish and UN pale brown in colour. Two lines in cell in UNF donot converge at the lower end. Central line crosses vein 2 much nearer the veins end

								than its origin. UNH with six prominent ocelli.
6.	*Lethe mekara* (Moore, 1858)	Common Forester	Red	75 mm	65-75 mm	600-1400 m	Upto 2100 m	UP of male is glossy olive brown while that of female is rufescent brown. UN of male is traversed by two lines. UN of female similar, however, white macular band runs on the UNF, cutting through the median brown band in its upper half. UNH of both the sexes consists of six ocelli placed on a broad pale band near the margin. The last ocellus double-pupilled.

7.	*Lethe chandica* (Moore, 1858)	Angled Red Forester	65-75 mm	70 mm	1100-1200 m	300 – 1500 m	UP is dark brown while UN is dab brown. The UN is traversed by two irregular wavy lines. The outer line is angled in UNH and points outward. The ocelli in UNH are irregular. The first ocellus lying in the apex is the largest.
8.	*Lethe insana* (Kollar, 1844)	Common Forester	60-65 mm	55-60 mm	2050-2550m	1500-2500m	UPF greenish brown. UNF lined with obscure white band. The band is more prominent in female than in male. The UNF has two bars in mid-cell and three apical ocelli. UNH with six apical ocelli. The first and second-last eyespot prominent and identical.

9.	*Lethe baladeva* (Moore, 1866)	Treble Silverstripe	60 mm	55-65 mm	1950-2300 m	1800-2300m	UNF with four white straight bands of which third from the base is silvery. The ocelli in the UNF are of equal size and placed in a straight row. UNH with two silvery bands and with six prominent ocelli.
10.	*Lethe dura* (Moore, 1892)	Scarce Lilacfork	83-85mm	70-85 mm	1850-1950m	1800-2200 m	UPF with pale borders in male with prominent ocelli. Central band in the UNH widens near leading edge. Inner edge of central band on UNH angled in between veins 4 and 6.
11.	*Lethe maitrya* (de Nicéville, 1881)	Barred Woodbrown	50 mm	45-55 mm	2250-3150m	2500-3800m	Whitish bars on UNF and white-edged wavy brown bands in UNH.UN 4 apical ocelli in a straight line. All ocelli are equal in size. UNH yellowish rings surrounding ocelli absent.

12.	*Lethe sidonis* (Hewitson, 1863)	Common Woodbrown	60-70mm	58-70 mm	1850-3150 m	1200-3100 m	UP dirty brown. FW with an obscure post-discal line and subapical pale costal spot. HW not prominently toothed with three small black post-discal spots. UNH with six ocellar spots of which the upper and lower more prominent and submarginal lilac line narrow in front and behind.
13.	*Lethe nicetella* (de Nicéville, 1887)	Small Woodbrown	48-50mm	45-50 mm	2650-2750 m	1820-3000 m	UP golden-brown. Lack of sub apical ocelli in the underside forewing in males with a medial and a subapical spot in female large and white. UNH ocelli are subequal with ocellus in 3 and 4 blurred.

Cho et al. (2016). The specimen stored in the refrigerator becomes brittle and dry. Therefore, prior to the morphological examination, the specimens were relaxed by moistening in a hot water bath. The relaxed specimens were stretched by pinning the wings and thorax in the stretch board. The specimens were allowed to dry for about 24 hrs. Morphological features of the stretched and dried specimen were examined by referring to standard literatures (Evans, 1927; Haribal, 1992; Kehimkar, 2016). Data on wing size, wing structure, coloration and venation of each specimen were taken. Wings of two specimens of each species were clipped and stored in paper envelope, while the bodies (that would be used for DNA extraction) were preserved in a vial dipped in 70% ethanol at -20^{0}C in a refrigerator. All specimens collected (whole specimen or wings only) are kept in the repository of the Department of Zoology, Sikkim University.

6.2.3 DNA isolation, amplification and sequencing

Total genomic DNA is generally extracted from single leg of butterfly specimens (Hebert et al., 2004; Peña et al., 2011) but DNA extraction from legs was not satisfactory in the present study as the amount of DNA extracted was very less and insufficient for amplification purpose. Therefore, thoracic muscles of the butterfly specimen were used to extract DNA (Chen et al., 2020). Prior to DNA extraction, the thorax was cleaned with phosphate-buffered saline to remove all the minute scales that covers the thorax. The exoskeleton (cuticle) of the thorax and the muscles were separated using sterile forceps and scissors. The muscles were then ground using phosphate-buffered saline for the extraction of DNA. QIAGEN DNeasy Blood & Tissue kit was used to extract total genomic DNA following standard protocol provided in the kit by the manufacturer

(Qiagen, Germany). Polymerase chain reaction (PCR) amplification of the isolated genomic DNA in triplicates (3 samples for each target gene) was performed by targeting three gene regions: one mitochondrial genome *(COI*) and two nuclear genes (*Wg* and *EF1a*). These gene regions show high rate of substitution in the Lepidoptera and, hence, is considered ideal for resolving species level phylogeny (Sutrisno, 2006). Utility of the three gene regions in phylogenetic studies of Lepidoptera has been widely accepted and substantial sequences of the genes already exist in the database (Cho et al., 1995; Aduse-Poku et al., 2015).

PCR was performed using a Gradient Palm Cycler (Genetix, New Delhi, India) and ProFlex PCR system (Thermo Fisher Scientific, United States of America) with a total reaction volume of 25 µl (dH20 = 18µl; taq buffer = 2.5 µl; taq polymerase = 0.5µl; dNTPs = 1µl; forward primer = 1µl; reverse primer = 1µl; DNA sample = 1µl). The PCR condition used for amplification was 98°C for 8 min (initial denaturation); 35 cycles of 94°C for 1 min (denaturation), 45-60°C for 1 min (annealing) (depending on the primer sets), 72°C for 1 min (extension); 72°C for 10 min (final elongation)(**Table 6.2**). PCR products were purified with the help of Gene Elute PCR clean up kit (Sigma-Aldrich) following manufacturer's protocol. Purified PCR products were then outsourced for sequencing to Macrogen, Korea.

Table 6.2: Details of the primers used for molecular analysis of *Lethe* butterflies recorded from Sikkim, eastern Himalaya.

Gene region	Primers	Sequence	Annealing Temperature	Authors
Cytochrome Oxidase I (COI)	Lep F1	ATTCAACCAATCAT A AAG ATA TTG G	50^{O}C	Hebert et al., 2004
	Lep R1	TAAACTTCTGGATG TCCAAAAAATCA		
Wingless *(Wg)*	LepWG1	GARTGYAARTGYCA YGGYATGTCTGG	45^{O}C	Brower & DeSalle, 1998
	LepWG2	CTICGCARCACCART GGAATGTRCA		
Elongation factor-1 α *(EF-1α)*	M3	CACATYAACATTGT CGTSATYGG	60^{O}C	Cho et al., 1995
	rcm4	ACAGCVACKGTYTG YCTCATRTC		

6.2.3 Blast analysis, sequence retrieval and alignment

The sequenced gene region was first assessed for quality check using Sequence Scanner Software (version 2). Out of the three gene regions, only *COI* yielded good result while *EF1a* and *Wg* yielded fragmented sequences. The trace score (measured using SequenceScanner) of *EF1a* and *wingless* were relatively lower (<30). Hence, only *COI* was considered for phylogenetic analysis. Altogether, 11 sequences of *COI* region of 9 species were successfully generated during the study. The sequencesof four species (*Lethe sinorix, Lethe chandica, Lethe mekara, Lethe kansa*) could not be generated due to low DNA yield. The 11 *COI* sequences so generated are submitted in the National Centre for Biotechnology Information (NCBI) repository (**Table 6.3**). For similarity search, I performed blast analysis for *COI* genes of butterflies under genus *Lethe* using the NUCLEOTIDE BLAST suite of NCBI (www.ncbi.nlm.nih.gov). Sequences of *COI* gene regions available at the NCBI for different species of *Lethe* (a total of 24 species) from different geographical regions were retrieved from the NCBI nucleotide database. Altogether, the sequences of 27 species (including those that were sequenced in this study) were compiled for the phylogenetic analysis (**Table 6.3**). The nucleotide sequences were aligned using Clustal omega program (http://www.ebi.ac.uk/Tools/msa/clustalo/) from EMBL-EBI website. The aligned sequences were manually edited using the tool BioEdit version 7.2.5 (Hall, 1999) to trim the unaligned portions.

6.2.4 Phylogenetic analysis

Prior to the phylogenetic analysis, best fit nucleotide substitution model for our dataset was determined by jModelTest program 2.2.10 using the corrected Akaike Information Criterion (Posada, 2008). Out of the various models, GTR (Generalized Time Reversal) +I (Invariant sites) +G (Gamma) was found to be the best fit model. To assess the phylogeny of *Lethe,* I used Bayesian Inference approach of phylogeny using MrBayes version 3.2.7 (Huelsenbeck & Ronquist, 2001) with Markov Chain Monte Carlo (MCMC) run for 5 million generations sampling every 100th generation. Branch support was evaluated with Bayesian posterior probabilities (BPP). Most of the tribes under subfamily Satyrinae forms an in-group, therefore, I rooted the phylogenetic tree using a nearest polyphyletic sister taxa, *Brassolis sophorae* (Morphinae, Brasolini) (Peña et al., 2011). The resulting phylogenetic tree was visualized using FigTree version 1.4.3.

6.2.5 Divergence time estimation

Divergence time of *Lethe* was estimated using Bayesian MCMC approach in Bayesian Evolutionary Analysis Sampling Trees Program (BEAST) version 2.6.3 (Bouckaert et al., 2014). Prior to divergence time estimation, a configuration file in XML format was created in BEAUti, a part of BEAST package. The file contains all the necessary information such as (i) aligned sequence data, (ii) model specification (iii) initial values and parameter constraints and (iv) MCMC algorithm required for running an analysis in BEAST. GTR was selected as the substitution model along with Gamma category count set to 4. To model the rate of molecular evolution, I used relaxed log normal molecular clock and calibrated Yule model of speciation. Tree calibration was done using two secondary calibration points, based on divergence time of outgroups provided in Peña et al. (2011). First I constrained the divergence time of *Brassolis sophorae* and *Elymnias casiphone* to 33 ± 0.5 Mya (Million years ago) with a normal distribution. As the second calibration point, I used the age of the split of *Coenonympha pamphilus* and *Coenonympha thyrsis* (4.3±0.5 Mya); which are closely related to *Lethe* group. The analysis was run for 40 million generations with a burn-in at every 1000th generation. The resultant log output was analyzed with Tracer version 1.7.1 to inspect ESS of the parameters. The individual post burn-in trees generated were summarized into one Maximum Clade Credibility (MCC) tree using Tree Annotator version 2.6.3. Finally, the MCC tree was visualized in FigTree version 1.4.3.

Table 6.3: Details of the species of *Lethe*used for molecular analysis. Specimens collected during the study are marked as asterisk (*). NCBI accession numbers of gene (*COI*) sequences along with details of the region of collection is provided

Species	**Gene bank accession number**	**Region of Specimen collection**
Lethe rohria	KY354195.1	Western Ghats, India
Lethe rohria	JN797788.1	Mizoram, India
Lethe rohria	KJ459776.1	Western Ghats, India
Lethe rohria	KC158411.1	Pakistan
Lethe syrcis	EF545700.1	China
*Lethe insana**	MT886716	Rangeet Valley, Sikkim, India
*Lethe insana**	MT886715	Rangeet Valley, Sikkim, India
Lethe sicelis	KF491831.1	Japan
Lethe sicelis	LC541741.1	Japan
Lethe satyrina	KM111637.1	China
*Lethe verma**	MT886709	Rangeet Valley, Sikkim, India
Lethe verma	KC158414.1	Punjab, Pakistan
Lethe verma	KC158413.1	Pakistan
Lethe verma	KC158412.1	Ajk, Pakistan
Lethe verma	HQ990376.1	Pakistan
*Lethe nicetella**	MT886706	Rangeet Valley, Sikkim, India
*Lethe maitrya**	MT886716	Rangeet Valley, Sikkim, India
*Lethe sidonis**	MT886708	Rangeet Valley, Sikkim, India
*Lethe latiaris**	MT886711	Rangeet Valley, Sikkim, India
Lethe kansa	EF597536.1	Yunnan, China
Lethe dura	NC026062.1	China
Lethe dura	KF906485.1	-
*Lethe dura**	MT886710	Rangeet Valley, Sikkim, India
Lethe chandica	MK348952.1	Lawchara National Park, Bangladesh
Lethe chandica	EF597533.1	Anhui, China
Lethe marginalis	JX185825.1	Korea
Lethe confusa	JN797786.1	India

Lethe confusa	EF597534.1	Yunan, China
*Lethe confusa**	MT886713	Rangeet Valley, Sikkim, India
*Lethe sp**	MT886716	Rangeet Valley, Sikkim, India
Lethe confusa	KM207097.1	China
Lethe confusa	KM244658	China
Lethe confusa	KF226515.1	Malaysia
Lethe minerva	DQ338768.1	Bali, Indonesia
Lethe kansa	KM111636.1	China
Lethe diana	GU696005.1	South Korea
Lethe diana	JX185824.1	South Korea
Lethe diana	KM111635.1	Jiju, South Korea
Lethe andersoni	EF545699.1	Yunan, China
*Lethe baladeva**	MT886712	Rangeet Valley, Sikkim, India
Lethe uemurai	NC050915.1	Qinling Mountain, Shaanxi, China
Lethe uemurai	MN611537.1	Qinling Mountain, Shaanxi, China
Lethe helle	MN611529.1	Badagongshan National Reserve, Hunan, China
Lethe baileyi	NC050905.1	Qinling Mountain, Shaanxi, China
Lethe nigrifascia	NC050910.1	Qinling Mountain, Shaanxi, China
Lethe hayashii	NC050907.1	Qinling Mountain, Shaanxi, China
Lethe satyrina	KM111637.1	Hupingshan National Nature Reserve, Hunan, China
Lethe oculatissima	NC050911.1	Qinling Mountain, Shaanxi, China
Lethe andersoni	EF545699.1	China
Lethe baucis	NC050906.1	Badagongshan National Reserve, Hunan, China
Lethe marginalis	JX185825.1	South Korea
Lethe marginalis	NC050909.1	Badagongshan National Reserve, Hunan, China

6.3 Results

6.3.1 Morphological identification

The morphological characters of the collected butterfly specimens were assessed following Evans (1927), Haribal (1992) and Kehimkar (2016). The details of the key identifying characters along with elevational range of the 13 species recorded during the study (**Photo plate 6.1**) are provided in **Table 6.1**.

6.3.2 Phylogenetic inference

We recovered around 584-659 bp of mitochondrial *COI* of the nine species (*L. verma, L. confusa, L. insana, L. latiaris, L. baladeva, L. dura, L.maitrya, L. sidonis, L. nicetella*) and 11 specimens under genus *Lethe* out of which sequences of six species were novel (*L. insana, L. latiaris, L. baladeva, L.maitrya, L. sidonis, L. nicetella*). The target fragment of 580 bp of *COI* for each of the species was used for the phylogenetic analysis. The sequences have been submitted in the GenBank database (NCBI) and accession number of the same has already been acquired. The phylogenetic tree of *Lethe* based on *COI* gene (580 bp of 27 species comprising sampled and retrieved sequences from NCBI) was generated using Bayesian Inference (**Figure 6.1**).The high posterior probability values (>90%) indicated good support for most of the nodes. Based on the result of this study, genus *Lethe* was recovered as monophyletic group comprising two distinct monophyletic clades. Clade I consist of various species with three distinct sub-clades comprising of (i) *L. hayashii, L. syrcis, L. baladeva, L. marginalis, L. andersoni, L. sicelis, L. titania, L. baucis, L. insana, L. oculatissima, L. minerva, L. latiaris, L. kansa, L. chandica* and *L.*

diana group, (ii) *L. verma, L. confusa* and *L. satyrina* group, and (iii) *L. rohiria* as a separate group. Sub-clades i and ii shares a common ancestor separated from *L. rohiria* group. The second clade (Clade II) is represented by species such as *L. sidonis*, *L. nicetalla*, *L. maitrya* (the woodbrowns) groups and *L. uemurai*, *L. helle* and *L. dura* group. The woodbrown group represents a cryptic association with similar morphological and ecological characteristics.

7.3.3 Time of Divergence

Divergence time estimation through BEAST analysis showed the ancestors of genus *Lethe* and *Coenonympha* diverged at around 24 Mya (± 8 Mya) during late Oligocene epoch. The major divergence of the genus *Lethe* was only observed at around 20.27 Mya (±7 Mya) when the genus separated into two distinct clades. The separation of clades into distinct monophyletic groups is perhaps one of the major events in evolutionary history of the genus. Clade I rapidly started diversifying after 20 Mya (±6 Mya), while in Clade II, major divergence event occurred only at around 10.37 Mya (±4 Mya) during the late Miocene. Many of the present day species under the genus could have originated during the late phase of this period (10-6 Mya). Some species e.g., *L. helle, L. uemurai*, *L. maitrya, L. nicetella*, *L. sidonis*, *L. baileyi*, *L. nigrifascia* showed recent origin during the Pliocene epoch (6-2.5 Mya). Among all the species under the genus, *L. helle* and *L. uemurai* represents the most recent stock whose speciation occurred at around 0.9 Mya (± 0.1 Mya).

Figure 6.1: Phylogenetic tree of genus *Lethe* based on *COI* gene using Bayesian Inference approach. The colour signifies different clades and sub clades. Values on the node represent the posterior probability value.

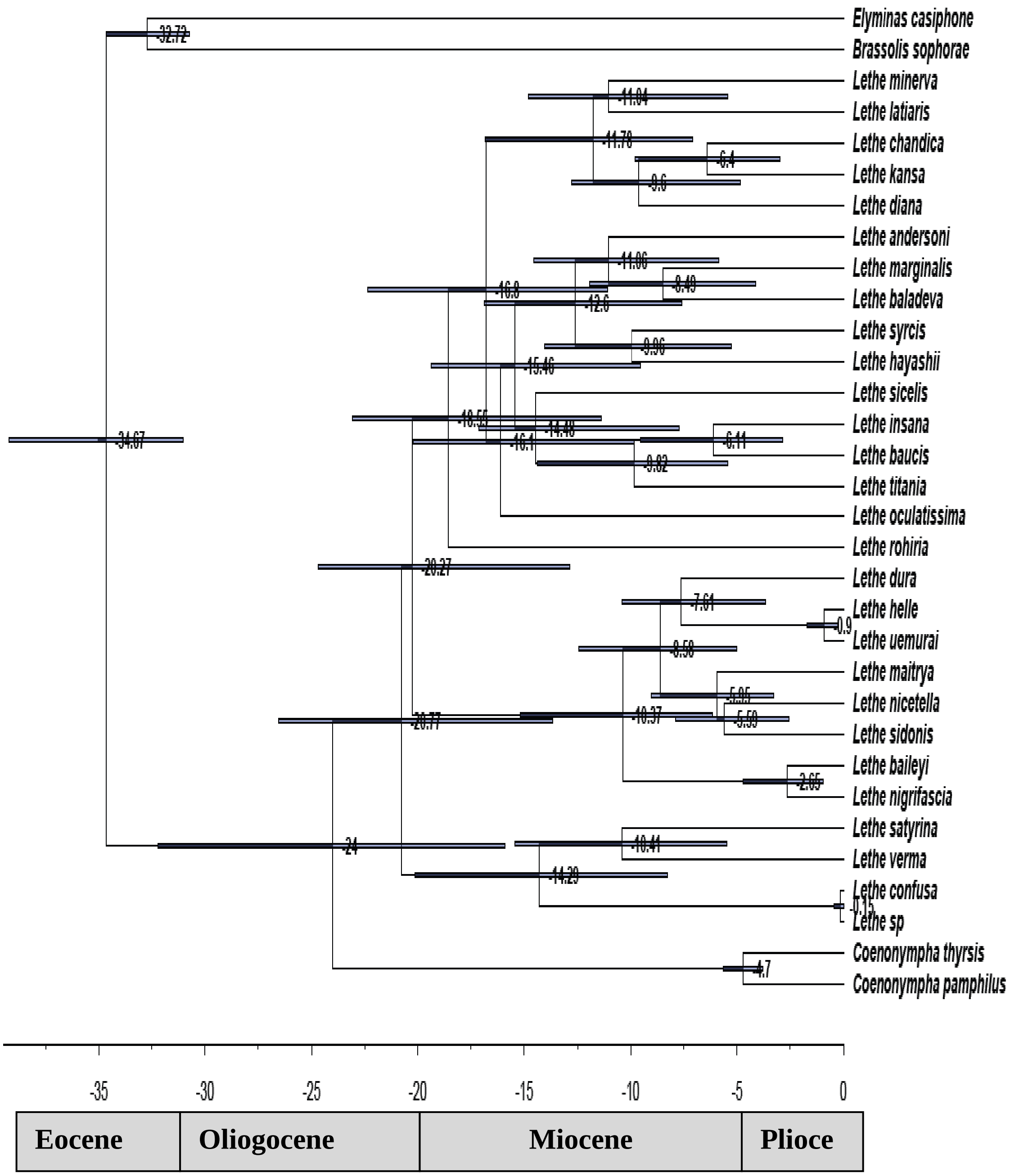


Figure 6.2: Tree derived from BEAST showing time of divergence of butterfly genus *Lethe*. The time line is scaled in million years (Mya). The number in the nodes represents time of divergence in Mya.

6.4 Discussion

6.4.1 Phylogeny of genus *Lethe*

The collected specimens of genus *Lethe* could be well identified based on morphological characteristics. The shared morphological characteristics of many species indicate the presence of distinct taxonomic clusters within the genus. However, discrepancies between different taxonomists in classification of the genus based solely on morphological features indicate that the taxonomy of *Lethe* has not been well resolved (Fruhstofer, 1911; Lesse, 1957; Lang, 2017; Das et al., 2020). The use of molecular markers (*COI*) aided in validating the morphological identification and differentiating cryptic taxa such as *Lethe sidonis* and *Lethe nicetella* because resolving taxonomy by relying only on morphological characters was difficult in these species (de Nicéville, 1887). Further, the use of molecular markers was crucial in understanding the nature of relationship between different species in the genus (Chen et al. 2020).

For phylogenetic reconstruction, I had considered two nuclear genes (*Wg* and *EF1a*) and one mitochondrial gene (*COI*). Only *COI* yielded good quality sequences and was further considered for phylogenetic analysis in this study. Depending solely on barcode gene (*COI*) for molecular taxonomy has received criticism *(*Elias et al., 2007) and inclusion of other gene markers increases the efficiency of understanding deep rooted phylogeny of butterflies (Peña et al., 2006). However, the t result of the present study (based on 580 bp of *COI*) is at par with the phylogeny of the genus based on entire mitochondrial genome (Chen et al., 2020). Based on the phylogeny of 14 species, Chen et al. (2020) showed that the genus *Lethe* consists of a monophyletic group comprising two clades;(I) *baladeva,minerva, marginalis, oculatissima, and satyrina* groups, and (II) *sura* group. Consistent with the findings of the study, present result supports the monophyly of the genus and two clades distinction. The similarity in results indicates that partial mitochondrial gene i.e, *COI* is as efficient as the whole genome in ascertaining the phylogeny of genus *Lethe*.

One of the significant findings of this study is the placement of several species in clade I which differed significantly with the classification of the genus proposed by Lesse (1957). Based on genitalia and several morphological features Lesse (1957) classified *Lethe* into 16 groups namely, *sura, europa, dynsate, samio, satyrina, oculatissima, minerva, baladeva, gracilia, sicelis, lataris, trimacula, eurydice, portlandia, gemina* and *manzorum*. *L insana* and *L. baucis*were previously placed in *satyrina* group along with *L. verma, L. satyrina* and *L. confusa*. Contrary to the previous placement, it was observed that *L. verma* and *L. confusa* forms a distinct monophyletic sub-group within the first group (Clade I). While *L. insana* and *L. baucis*shared lineage with *L. sicelis* indicating that these species rather belonged to *sicelis* group. Another noteworthy finding of the present study is to delineate shared ancestry of *L. kansa*with the member of *minerva* group as this species was previously thought to be the member of *sanio* group. Similarly, other species in *minerva* group, e.g *L. titania* shared more ancestral similarities with the member of *sicelis* while *L. marginalis* belonged to *baladeva* group. Based on the present findings I suggest that the Clade I of genus *Lethe* should be broadly classified into three sub-clades rather than grouping species into many smaller groups based on shared morphological similarities.

6.4.2 Diversification, historical-biogeography and Himalayan colonization

The *verma, confusa, satyrina* groups shows early divergence in the BEAST tree but this group is a distinct lineage of Clade I as per the Bayesian phylogenetic tree. The incongruence between BEAST analysis and the tree based on Bayesian inference has also been reported by Pena et al. (2011). Nevertheless, the BEAST results do show a pattern in origin and divergence in genus *Lethe*. The ancestors of *Lethe* originated at around 24 Mya (± 8 Mya) during the Oligocene. Pena et al. (2011) suggest the origin of ancestor of genus *Lethe* in the Eastern Palearctic region even though extant species are much diverse in the Oriental region. The hypothesis of Palearctic origin is further supported by the recent discovery of *Lethe corbieri* in Oligocene deposits of South-Eastern France (Nel et al., 1993). The divergence of the genus into two distinct clades marks the major event in the evolution and diversification of *Lethe*. The divergence of the two clades indicates a major separation in niche occupation. The distribution of most of the species in clade II above mid elevation suggests that the ancestors of the group may have diversified in the cooler environments. The presence of many extant taxa of clade I in the low to mid elevation in South-East Asia indicates that the ancestors of this clade occupied the hot tropical climate and diversified there in..

After clade differentiation, the genus may have then colonized parts of East Asia and radiated therein through various dispersal or vicariance events. The lack of genetic sequences of many extant species makes it rather difficult to test the two hypotheses(dispersal and vicariance processes) of speciation. The radiation of the genus (irrespective of the mode of speciation) in the Asian region was probably favored by change in climatic regime in the Miocene epoch that caused the expansion of grasses. The tribe Satyrinae, under which genus *Lethe* belongs, diversified with the ability to feed on grasses in the Oligocene (Peña & Wahlberg, 2008). The expansion of grassland during Miocene created novel niches and provided special opportunity for the tribe to flourish globally (Peña et al., 2011). The colonization of *Lethe* in the Himalayan region, however, may have occurred only in the late Miocene. Branching of *L. verma* and *L. confusa* in our data shows that the population in the Himalaya is comparatively new stock than the populations of other South Asian countries. Further, most of the extant taxa of *Lethe* are more diverse in the Eastern Himalayan region and surrounding countries. This indicates that the species may have dispersed form East Asia and through upward westward movements began colonizing the lowlands of newly rising Himalaya. Expansion of the grasses in the Himalayan region in the late Miocene (Singh et al., 2011) favored colonization process in *Lethe*. In the Asian region, subsequent uplift of Himalaya post Miocene (15 Mya) played a crucial role in intensification of South Asian Monsoon (SAM) (Molnar et al., 2010). Variable climatic conditions followed by forest fire favored expansion of grasses in the Himalaya (Srivastava et al., 2018) creating favorable niche environment for *Lethe* to flourish.

"*Vertical colonization*" processes, wherein highlands would be colonized by the elements arising from the lowlands as a result of cold environmental adaptation, have been suggested as plausible explanation for current assemblages of species in the mountains (Lobo & Halffter, 2000; daSilva, 2018a). According to this hypothesis, the species that exist between different elevational ranges in the mountains would be closely related.

Among butterflies, *Ithomolia* is the most potent example of vertical speciation along the elevational gradient (Hall, 2005). Majority of the butterfly species in the genus *Lethe* are found in low or mid elevation sites and few species occupy cooler temperate niche in the Himalaya (Kehimkar, 2016). Within genus *Lethe*, the divergence of *L. sidonis* and *L. nicetella* is an example of vertical speciation along the elevation. *L. sidonis* is found all over Himalaya while *L. nicetella* is restricted to Sikkim and adjoining Bhutan in the eastern Himalaya and occupies slightly higher elevation than *L. sidonis*. *L. nicetella* might have originated in the eastern Himalayan region after diverging from the ancestral *L. sidonis* stock during the early Pliocene and would have colonized higher elevation niches than its ancestors. The divergence estimation reveals that the temperate clades as a whole have separated from the other clades much before the colonization event in the Himalaya. Further, the presence of the *Lethe* all over South-East Asia and East Asia reveals that speciation event in the genus may have been a complex mechanism. Additional study with distribution records and genetic sequence of many extant *Lethe* species is required to fully comprehend the phylo-biogeography of this genus.

6.5 Conclusion

The phylogeny of genus *Lethe* was analyzed using the gene sequence of mt*COI*. The use of molecular marker aided in validating the morphological identification and resolving the taxonomic classification of the Genus. Divergence time estimation analysis reveals that *Lethe* probably originated at about 24 Mya (±8 Mya) in Oligocene and diverged in two distinct clades at around 20.27 Mya (±7 Mya). The divergence of the ancestral Lethe in two clades allowed each clade to occupy separate niches. . In general, the radiation of

Lethe was mainly driven by radiation of grasses. The present day distribution of different species of *Lethe* was probably driven by several vicariance and dispersal mechanism. The divergence and distribution of *Lethe nicetella* and *L. sidonis* presents a clear case of vertical speciation mechanism in the mountains. However, in order to get more insights in the role of evolutionary processes in effecting the present day distribution of *Lethe*, more phylo-biogeographic studies are necessary.

Lethe verma

Lethe confusa

Lethe kansa

Lethe sinorix

Lethe insana

Lethe dura

Lethe latiaris

Lethe mekara

Lethe maitrya

Lethe baladeva

Lethe sidonis

Lethe nicetella

Photo plate 6.1: Photo showing *Lethe* specimens collected for molecular analysis form Rangeet Valley, Sikkim.

CHAPTER 7

CONCLUSION AND CONSERVATION IMPLICATIONS

7.1 Summary and conclusion

Understanding why biodiversity varies across spatial gradients such as elevation is a decades old question in ecology, biogeography and conservation science. Information on distribution pattern of biodiversity and its underlying mechanism provide a valuable insightsin predicting the effect of climate change and habitat destruction (Hodkinson, 2005), and identifying conservation priority areas (Hunter & Yonzon, 1993;Bhardwaj et al., 2012). Studies around the world have shown that the pattern of diversity varies between taxa and region of study (Stevens, 1992; Sánchez-Rodríguez & Baz, 1995, Rahbek, 2005; Acharya et al. 2011a; Wu et al; 2013a; Li & Feng, 2015). Along the elevational gradient, diversity (α/β/γ diversity) may decrease linearly with elevation, peak at mid elevation, or increase with elevation (Rahbek, 2005; Kraft et al., 2011; Syfert et al., 2018; Hu et al., 2018; Castro et al., 2019; Naud et al., 2019).Factors affecting the pattern of biodiversity can be broadly grouped into contemporary climatic, biotic, evolutionary and spatial factors(McCain & Grytnes, 2010).

The butterflies are reported to follow all the three pattern of diversity along the elevational gradient. Studies in the Himalayan region have shown that species richness of butterflies decreases linearly with elevation while turnover increases with increasing elevational distance. Since the diversity trend may vary in regional and local scale, more studies on other gradients is necessary to understand the generality of the pattern. Additionally, the diversity pattern of different ecological sub-groups of butterflies had not been explored earlier. Lastly, the evolutionary history of butterflies that have shaped the current distribution of butterflies remain poorly explored in the Himalaya. Hence, this study originated (i) to understand the species richness pattern, range size distribution and turnover rate of butterflies along elevation gradient in Rangeet valley in Sikkim Himalaya,(ii) to understand the potential factors influencing the elevational pattern of butterflies, (iii) to explore the abundance trend of wide ranging butterfly species along elevation gradient and(iv) to understand the distribution pattern and phylogeny of some closely related species.

Sikkim is one of the small northeast states of India and part of Himalaya biodiversity hotspot. The state is traversed by two major river systems, the river Teesta and its tributary Rangeet. Rangeet valley lying in the south and west district, represents a large catchment areas that expands from 300m to 8586m (summit of Mount Khangchendzonga, third highest mountain in the world). The valley experiences wide range of climatic condition from hot/ humid tropical climate in lower valleys, cool temperate climate in mid elevation to alpine tundra in the high elevation. The vegetation structure also changes with continuous gradation of climate. The vegetation type prevailing in this region show rapid transition at approximately 900m elevation (Haribal 1992; Acharya & Sharma, 2013).

The present study was conducted in the Rangeet valley covering a total elevational range of 3300m (300m-3300m). Fixed width point count method was used to sample butterflies along transects established along 16 elevational zone. Butterflies were sampled for two years (2016 to 2018) covering three main seasons; pre-monsoon (March-May), monsoon (June-August) and post-monsoon (September-November). The butterfly counts were conducted for 3-4 times in each transects per season. The butterflies recorded were categorized into different sub-groups according to families, range size, bio-geographic affinity and host plant specialization. Data on several predictor variables such as tree species richness, tree density, shrub species richness, shrub density, actual-evapotranspiration (AET), normalized difference in vegetation index (NDVI) and area were taken through primary sampling or by accessing secondary sources.

A total 3573 individual butterfly representing 253 species and six families were recorded after the completion of 1860 point counts. Species richness and density of overall butterflies declined linearly with increasing elevation. Richness and density was highest at the lower elevation zone (<500m). Species richness of majority of sub-groups (except for Riodinidae and Palearctic species) followed a declining trend along the elevation. Density of the sub-groups also showed similar trend. Actual evapotranspiration was the most crucial factor affecting species richness pattern and density of overall butterfly community and majority of the sub-groups. Tree density and species richness also affected the species richness pattern of butterflies in the study. Shrub density explained much of the variation in density along the elevational gradient. The effect of habitat variables varied among the different sub-groups.

Along the elevation, beta diversity (incidence based and abundance based) showed a peak at mid elevation coinciding with major shift in vegetation type. Both the incidence and abundance based dissimilarity increased significantly with an increase in the elevational distance between sites. The high turnover in butterfly assemblages indicates that each elevational zone is distinct along the gradient. Partitioning of beta diversity revealed that turnover (in case of incidence based measure) or the balanced variation (in case of abundance based measure) component contributed more to the overall beta diversity. Environmental variables explained a large proportion of variance observed in beta diversity pattern. Among the sets of environmental variables, variation in AET between the elevational zones had the most crucial contribution in the beta diversity pattern followed by difference in tree richness and density. The trait based analysis revealed species assemblages of butterflies along elevation according to biogeographic affinity. The highland butterflies were mostly composed of Palearctic species while the lowland species were mostly affiliated to butterflies of Oriental region.

In the Rangeet Valley, about 90.11 % of the butterflies had range size lesser than 1500m and among them40% were restricted to single elevation zone. The mean elevational range size of butterflies differed significantly among family level and biogeographic affinity. Among dtheifferent families, Nymphalidae had the highest elevational range. In terms of biogeographic affinity, Palearctic butterflies had the largest elevational range as compared to other sub-groups. The mean elevational range of butterflies increased significantly with elevation conforming to Rapoport’s rule. Similar trend was observed in sub-groups such as Nymphalidae, Papilionidae, Lycaenidae, Oriental, Global, oligophagous and polyphagous species. The total density of butterfly species was positively correlated with their elevational range. A total of 10 species had the highest elevational range and their density pattern showed varying response to elevation. Straight Banded Treebrown (*Lethe verma*) and Dark Judy (*Abisara fylla*) showed a mid hump pattern, Indian Red Admiral (*Vanessa cardui*) and Pea Blue (*Lampides boeticus*) showed increasing trend while pattern of Red Helen (*Papilio helenus*) and Striped Blue Crow (*Euploea mulciber*) followed decreasing trend with elevation. Density of Indian Tortoiseshell (*Aglias caschmirensis*) increased significantly from middle elevation to the higher elevation. The density of Indian Cabbage White (*Pieris canidia)* and Yellow Spot Swift (*Polytremis eltola*) did not show any significant trend. The density pattern of each butterflies were explained by different sets of environmental and spatial variables probably due to the differences in their life history traits.

Phylogenetic analysis based on mt*COI* indicated that *Lethe* originated at around 24 Mya (± 8 Mya) in Oligocene period. The genus diverged in two distinct clades at around 20.27 Mya (±7 Mya) and then radiated by occupying two distinct niche spaces; Clade I occupied lowland tropical habitat while Clade II were adapted to temperate habitats. The genus may have then colonized parts of east Asia and radiated therein in the Miocene epoch probably favoured by the expansion of grasses. Time of divergence analysis revealed that the Himalayan stock (*Lethe verma* and *Lethe confusa*) were comparatively new than their counterparts occurring in other parts of Asia indicating that the colonization of *Lethe* in the Himalayan region would have taken place latter in late Miocene. While colonizing Himalaya, some diversified into new species through the process of vertical colonization e.g *Lethe nicetella* originated in the eastern Himalayan region after diverging from the ancestral *Lethe sidonis* stock during the early Pliocene.

The phylogeny and biogeography of *Lethe* provides an example of how evolutionary events shaped their current distribution pattern. Additional studies on phylogeny are needed to get more meaningful insights about the role of evolutionary process in shaping the distribution pattern of butterflies in the Himalayan region.

7.2 Conservation implication

Sikkim consists of 689 species of butterflies which is approximately 50% of the butterflies reported form Indian subcontinent. With a total of 253 species of butterflies (recorded during the study), Rangeet Valley represents a landscape with high butterfly diversity. Majority of the butterflies in the valley are found in the low elevation, some are even elusive and federally protected (Dewan et al., 2019). While moving along the elevation, species richness and density of butterflies decreases linearly with high turnover rates. High turnover in butterfly assemblages indicates that the butterfly community in each elevation is unique. Therefore, all elevational zones in Rangeet valley is important in conservation point of view as safeguarding the local community assemblage in each elevation is important in maintaining the regional butterfly diversity.

The Sikkim Himalaya represents 31% of the total geographical area under protected area network and most of these legal conservation areas lies above 1500m (FEWMD, 2019). Since butterflies are exclusively dependent on vegetation, existence of natural habitat ensures their long term conservation in the mid and high elevation. The record of a very rare and federally protected *Lethe nicetella* after 120 years at 2700m in this study indicates that the natural habitats are intact in and around this elevational zone. In a sharp contrast, the low land forest in the Himalaya experiences immense anthropogenic pressures as compared to higher elevation, leading to extinction of species (Pandit et al., 2007).The forest cover in lowland areas below 500m in Sikkim is only 36 km² (FSI, 2019) and only 6 km^2 lies under protected area network. Due to the rapid increase in mega power projects and industries (specifically pharmaceutical companies) since past two decades, much of forest area has narrowed extensively, and in many places reduced to fragmented patches at species rich lower elevation. The analysis of elevational range size distribution of butterflies revealed that majority of the restricted ranged species (specialized to thrive in a narrow niche) occurs in the lower elevation. . Additionally, butterflies of low elevation are also impacted due to global climate change. Therefore, the butterflies in the lower elevational are extremely threatened and need holistic conservation approach.

According to several reports, the range of butterflies has already shifted in Europe, North America and Australia due to the rising global temperature (Foristera et al., 2010; Braby & Hsu, 2019). There is evidence of elevational range shift in butterflies of the Sikkim Himalayan region. Many butterflies are now found in slightly higher elevation than their previous distribution (Acharya & Chettri, 2012). Due to variation in climatic tolerance, specialist species are adversely affected while generalist (due to their high tolerance capacity) can adapt and maintain their population (Platts et al., 2019). Changes in temperature and precipitation gradients will be a serious threat to small ranged species, oriental species and majority of the butterfly families. Additionally, monophagous species being exclusively dependent on single food plants are also threatened by habitat loss which will be accelerated by climate change (Fonseca, 2009). The variation in resilience and vulnerability are dependent on difference in life history associated with a particular group. Hence, exhaustive studies are required to document life history traits of various butterflies and to understand their response to the environment-elevation-gradient. Such studies will be crucial in providing information to formulate more specific conservation policies for different groups of butterflies.

In sum, suitable climatic conditions and heterogeneous habitats in the lower sub-tropical valleys of Rangeet supports high diversity of butterflies, making it the “hotspot” of butterfly diversity. Ironically, the lower elevations are also the area were butterflies are more threatened. The Government of Sikkim has taken an important step for ex-situ conservation of butterflies by proposing to establish a butterfly park (under consideration) at Rangrang, North Sikkim that would ensure the protection of lowland butterflies of the Sikkim Himalayan region. For the conservation of butterflies atthe landscape level, vast area of forest and protected areas are required. At present, Kitam Bird Sanctuary (6 km^2 area) is the only protected area below 1000m and is one of the most important areas for butterfly conservation in the lowland of Sikkim Himalaya. The sanctuary harbors rich diversity of butterflies along with many rare, federally protected and restricted ranged species (Dewan et al., 2019). However, the dominance of Chir Pine (*Pinus roxburghii*) monoculture in the sanctuary hinders the growth of natural vegetations that are also a host to many butterflies (Dewan et al., 2019). Planting and managing host and nectar plants of butterflies is necessary in this sanctuary to retain and conserve butterflies. Additionally, some site of the sanctuary can be declared as natural butterfly park. Long term monitoring of butterflies with the involvement of various stakeholders for assessment of nectar and larval host plants and capacity building of local communities would greatly contribute to the conservation of butterflies in this crucial protected area. Apart from natural forest, traditional agroecosystem has been proved to be important for conservation of butterflies (Sharma et al., 2020). The agroecosystem in Sikkim Himalaya consist of agricultural land interspersed within small patches of original forest. Safeguarding the original remnant patches of forest in consultation with the local communities is of outmost importance in order to conserve the native biodiversity. Prioritizing both natural forest and agroecoystem is necessary for conservation of butterfly diversity in the long run and in sustaining million years of evolutionary process that shaped current distribution of butterflies in the Himalayan region.

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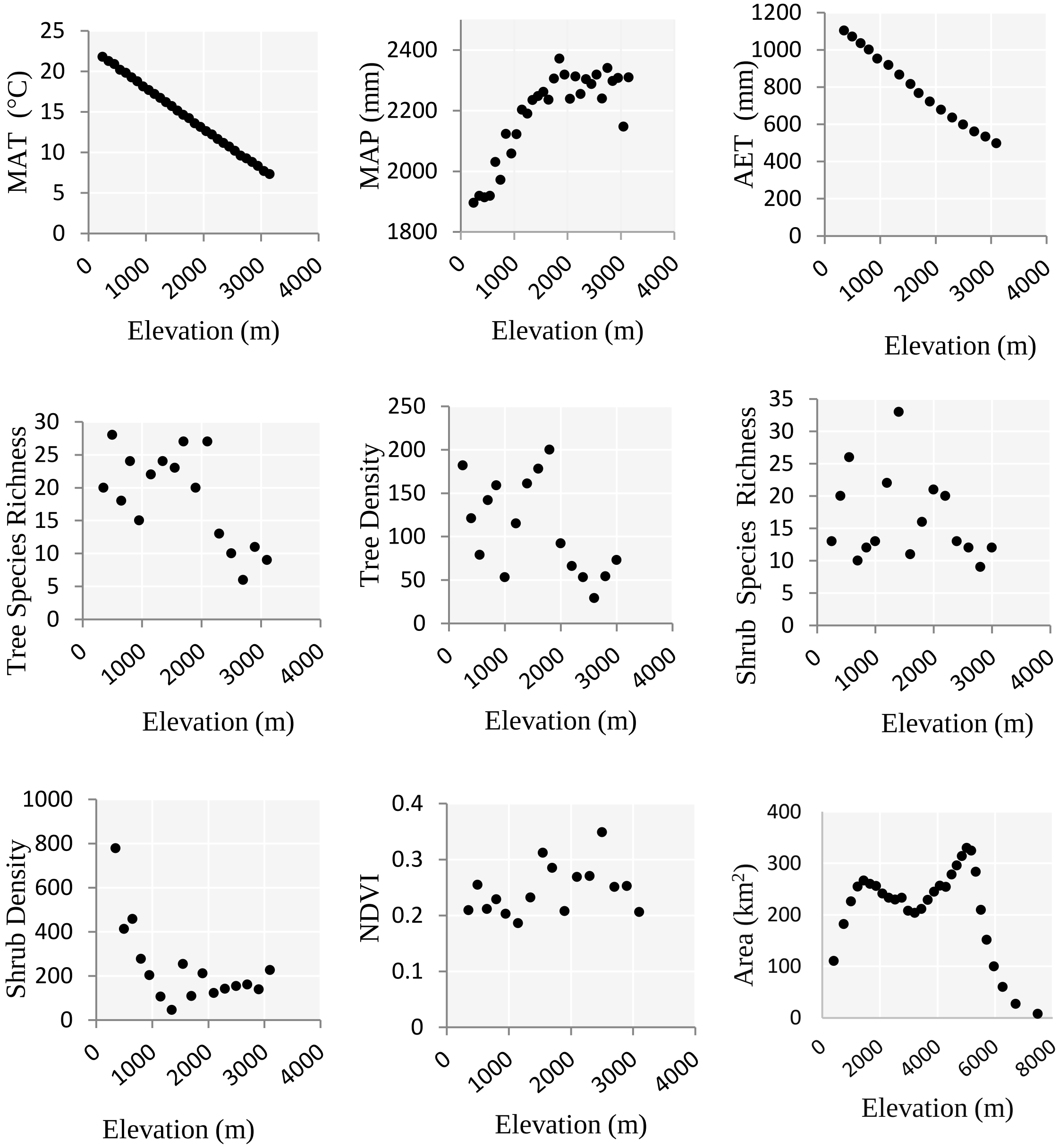
APPENDICES



FigureA.1: Scatter plot showing relationship between climatic, biotic and spatial variables with elevationin Rangeet Valley, Sikkim, Eastern Himalaya. MAT- Mean Annual Temperature; MAP- Mean Annual Precipitation; AET- Actual Evapotranspiration; NDVI- Normalized Difference Vegetation Index.

Table A.1: Details of the species recorded during the study in Rangeet Valley, Sikkim, Eastern Himalaya. OR- Oriental species; PA-Palearctic; GL- Global; SR- Small Range; LR- Large Range; MO-Monophagous; OL- Oligophagous; PL- Polyphagous; DD- Data Deficient.

Sl.No	Scientific Name	Common Name	Family	Biogeographic affinity	Range size	Range size category	Feeding guild	Wingspan (mm)
1	*Aeromachus jhora*	Grey Scrub Hopper	Hesperiidae	OR	900	SR	DD	25
2	*Aeromachus stigmata*	Veined Scrub Hooper	Hesperiidae	OR	550	SR	DD	26
3	*Baoris farri*	Paint Brush Swift	Hesperiidae	OR	100	SR	OL	45.5
4	*Boaris pagana*	Figure-of-8 Swift	Hesperiidae	OR	350	SR	DD	50
5	*Borbo bevani*	Lesser Rice Swift	Hesperiidae	African	100	SR	OL	34
6	*Burara jaina*	Orange Awlet	Hesperiidae	OR	100	SR	PL	65
7	*Capila jayadeva*	Striped Dawnfly	Hesperiidae	OR	100	SR	DD	70
8	*Celaenorrhinus munda*	Himalayan Spotted Flat	Hesperiidae	OR	100	SR	DD	47
9	*Celaenorrhinus putra*	Restricted Spotted Flat	Hesperiidae	OR	100	SR		50
10	*Celaenorrhinus ratna*	Ratna Flat	Hesperiidae	OR	100	SR	DD	43
11	*Coladenia indrani*	Tricolour Pied Flat	Hesperiidae	OR	100	SR	PL	43
12	*Erionota torus*	Rounded Palm-redeye	Hesperiidae	OR	100	SR	PL	70

13	*Gerosis phisara*	Dusky Yellow Breasted Flat	Hesperiidae	OR	100	SR	DD	40
14	*Gerosis sinica*	White Yellow Breasted Flat	Hesperiidae	OR	100	SR	DD	40
15	*Halpe filda*	Absent Ace	Hesperiidae	OR	800	SR		34
16	*Hasora badra*	Common Awl	Hesperiidae	OR	100	SR	OL	53
17	*Hasora chromus*	Common Banded Awl	Hesperiidae	OR	100	SR	PL	47
18	*Iambrix salsala*	Chestnut Bob	Hesperiidae	OR	600	SR	OL	34
19	*Korutahialos butleri*	Dark Velvet Bob	Hesperiidae	OR	100	SR	DD	28
20	*Matapa aria*	Common Redeye	Hesperiidae	OR	100	SR	MO	47.5
21	*Matapa sasivarna*	Black Veined Redeye	Hesperiidae	OR	100	SR	OL	43.5
22	*Notocrypta feisthamelii*	Spotted Demon	Hesperiidae	OR	950	SR	MO	44
23	*Notocrypta curvifascia*	Restricted Demon	Hesperiidae	OR	1350	SR	PL	43
24	*Ochus subvittatus*	Tiger Hopper	Hesperiidae	OR	150	SR	DD	23.5
25	*Odontoptilum angulata*	Chestnut Angle	Hesperiidae	OR	100	SR	PL	26
26	*Oriens gola*	Common Darlet	Hesperiidae	OR	100	SR	DD	25.5
27	*Oriens goloides*	Smaller Dartlet	Hesperiidae	OR	150	SR	OL	26

28	*Parnara* sp	-	Hesperiidae	OR				34
29	*Pelopidas conjuncta*	Conjoined Swift	Hesperiidae	OR	100	SR	OL	48.5
30	*Pelopidas mathias*	Small Branded Swift	Hesperiidae	OR	600	SR	PL	35
31	*Polytremis discreta*	White Fringed Swift	Hesperiidae	OR	100	SR	DD	38
32	*Polytremis eltola*	Yellow Spot Swift	Hesperiidae	OR	1550	LR	MO	40
33	*Potanthus* sp	-	Hesperiidae	OR	800	SR	DD	26
34	*Pseudocoladenia dan*	Fulvous Pied Flat	Hesperiidae	OR	1350	SR	OL	43
35	*Pseudocoladenia festa*	Dull Pied Flat	Hesperiidae	OR	100	SR	OL	36
36	*Pseudocoladenia fatua*	Sikkim Pied Flat	Hesperiidae	OR	1400	SR	DD	40
37	*Sarangesa dasahara*	Common Small Flat	Hesperiidae	African	600	SR	OL	30.5
38	*Tagiades litigiosa*	Water Snow Flat	Hesperiidae	OR	450	SR	PL	40.5
39	*Tagiades menaka*	Spotted Snow Flat	Hesperiidae	OR	600	SR	DD	49
40	*Tagiades parra*	Multi-spotted Snow Flat	Hesperiidae	OR	150	SR	DD	53
41	*Zographetus satwa*	Purple and Gold Flitter	Hesperiidae	OR	300	SR	DD	31
42	*Acytolepis puspa*	Common Hedge Blue	Lycaenidae	OR	1550	LR	PL	31.5

43	*Arhopala centaurus*	Centaur Oakblue	Lycaenidae	OR	300	SR	PL	33.5
44	*Arhopala abseus*	Aberrant Oakblue	Lycaenidae	OR	100	SR	MO	51
45	*Arhopala amantes*	Large Oakblue	Lycaenidae	OR	600	SR	PL	57.5
46	*Arhopala eumolphus*	Green Oakblue	Lycaenidae	OR	100	SR	DD	47
47	*Arhopala* sp		Lycaenidae	OR	100	-	-	45
48	*Catapaecilma major*	Common Tinsel	Lycaenidae	OR	100	SR	PL	28
49	*Catochrysops strabo*	Forget Me Not	Lycaenidae	OR	100	SR	PL	30
50	*Celastrina lavendularis*	Plain Hedge Blue	Lycaenidae	PA	100	SR	DD	31
51	*Charana mandarinus*	Mandarin Blue	Lycaenidae	OR	300	SR	MO	42.5
52	*Cheritra freja*	Common Imperial	Lycaenidae	OR	100	SR	PL	40
53	*Chliaria kina*	Blue Tit	Lycaenidae	OR	600	SR	DD	27.5
54	*Chliaria othona*	Orchid Tit	Lycaenidae	OR	150	SR	OL	25.5
55	*Spindasis lohita*	Long-banded Silverline	Lycaenidae	OR	100	SR	OL	33
56	*Curetis bulis*	Bright Sunbeam	Lycaenidae	OR	100	SR	DD	40
57	*Deudorix epijarbas*	Cornelian	Lycaenidae	-	150	SR	PL	39
58	*Flos areste*	Tailless Plushblue	Lycaenidae	OR	100	SR	DD	42

59	*Heliophorus brahma*	Golden Sapphire	Lycaenidae	OR	950	SR	OL	34
60	*Heliophorus epicles*	Purple Sapphire	Lycaenidae	OR	1350	SR	OL	31.5
61	*Heliophorus tamu*	Powdery Green Sapphire	Lycaenidae	OR	200	SR	OL	37.5
62	*Hypolycaena erylus*	Common Tit	Lycaenidae	OR	2150	LR	PL	34
63	*Jamides alecto*	Metallic Cerulean	Lycaenidae	OR	1050	SR	OL	32
64	*Jamides bochus*	Dark Cerulean	Lycaenidae	OR	450	SR	OL	29.5
65	*Jamides celeno*	Common Cerulean	Lycaenidae	OR	800	SR	PL	28.5
66	*Lampides boeticus*	Pea Blue	Lycaenidae	-	2450	LR	OL	30
67	*Leptotes plinius*	Zebra Blue	Lycaenidae	GL	100	SR	PL	26
68	*Loxura atymnus*	Yamfly	Lycaenidae	OR	1200	SR	PL	38
69	*Maneca bhotea*	Slate Royal	Lycaenidae	OR	100	SR	DD	39
70	*Megisba malaya*	Malayan	Lycaenidae	OR	450	SR	PL	25
71	*Orthomiella pontis*	Straightwing Blue	Lycaenidae	PA	400	SR	DD	30
72	*Prosotas lutea*	Brown Lineblue	Lycaenidae	OR	100	SR	DD	26.5
73	*Prosotas nora*	Common Lineblue	Lycaenidae	OR	350	SR	PL	21.5
74	*Pseudozizeeria maha*	Pale Grass Blue	Lycaenidae	-	850	SR	PL	28

75	*Rapala nissa*	Common Flash	Lycaenidae	OR	1250	SR	PL	36
76	*Spalgis epius*	Apefly	Lycaenidae	-	150	SR	Carnivorous	25
77	*Spindasis syama*	Club Silverline	Lycaenidae	OR	100	SR	DD	33
78	*Surendra quercetorum*	Common Acacia Blue	Lycaenidae	OR	100	SR	PL	35
79	*Taraka hamada*	Forest Perriot	Lycaenidae	OR	1000	SR	Carnivorous	25
80	*Udara dilecta*	Pale Hedge Blue	Lycaenidae	OR	1950	LR	DD	30
81	*Zeltus amasa*	Fluffy Tit	Lycaenidae	OR	600	SR	MO	30
82	*Zizeeria karsandra*	Dark Grass Blue	Lycaenidae	-	1350	SR	PL	21
83	*Zizina otis*	Lesser Grass Blue	Lycaenidae	-	100	SR	OL	
84	*Abrota ganga*	Sergeant Major	Nymphalidae	OR	100	SR	DD	82.5
85	*Acraea issoria*	Yellow Coster	Nymphalidae	-	150	SR	OL	65
86	*Aglais cashmiriensis*	Indian Tortoiseshell	Nymphalidae	OR	2750	LR	OL	60
87	*Argynnis childreni*	Large Silverstripe	Nymphalidae	PA	1100	SR	MO	87.5
88	*Argynnis hyperbius*	Indian Fritillary	Nymphalidae	PA	1050	SR	PL	75
89	*Ariadne merione*	Common Castor	Nymphalidae	OR	1000	SR	PL	52.5

90	*Athyma cama*	Orange Staff Sergeant	Nymphalidae	OR	1350	SR	MO	70
91	*Athyma inara*	Colour Sergeant	Nymphalidae	OR	100	SR	MO	62.5
92	*Athyma opalina*	Himalayan Sergeant	Nymphalidae	OR	100	SR	OL	62.5
93	*Athyma perius*	Common Sergeant	Nymphalidae	OR	1550	LR	PL	65
94	*Athyma ranga*	Blackvein Sergeant	Nymphalidae	OR	450	SR	OL	65
95	*Athyma selenophora*	Staff Sergeant	Nymphalidae	OR	150	SR	OL	65
96	*Aulocera swaha*	Common Satyr	Nymphalidae	PA	400	SR	OL	65
97	*Bassarona durga*	Blue Duke	Nymphalidae	-	100	SR	DD	100
98	*Cethosia biblis*	Red Lacewing	Nymphalidae	OR	1250	SR	OL	57.5
99	*Charaxes arja*	Pallid Nawab	Nymphalidae	OR	450	SR	DD	70
100	*Charaxes athamas*	Indian Nawab	Nymphalidae	OR	600	SR	PL	70
101	*Chersonesia risa*	Common Maplet	Nymphalidae	OR	100	SR	DD	42.5
102	*Cirrochroa aoris*	Large Yeoman	Nymphalidae	OR	1200	SR	MO	85
103	*Cirrochroa tyche*	Common Yeoman	Nymphalidae	OR	1200	SR	DD	70
104	*Cyrestis thyodamas*	Common Map	Nymphalidae	OR	1550	LR	MO	55
105	*Danaus genutia*	Striped Tiger	Nymphalidae	GL	1200	SR	PL	86

106	*Discophora sondaica*	Common Duffer	Nymphalidae	OR	600	SR	OL	85
107	*Elymnias hypermnestra*	Common Palmfly	Nymphalidae	OR	150	SR	OL	70
108	*Elymnias patna*	Blue-striped Palmfly	Nymphalidae	OR	100	SR	OL	90
109	*Euploea algea*	Long-branded Blue Crow	Nymphalidae	OR	1200	SR	OL	97.5
110	*Euploea core*	Common Crow	Nymphalidae	OR	1000	SR	PL	90
111	*Euploea mulciber*	Striped Blue Crow	Nymphalidae	OR	1750	LR	PL	95
112	*Euthalia telchinia*	Blue Baron	Nymphalidae	OR	400	SR	DD	67.5
113	*Euthalia aconthea*	Common Baron	Nymphalidae	OR	100	SR	PL	70
114	*Euthalia lubentina*	Gaudy Baron	Nymphalidae	OR	100	SR	OL	65
115	*Euthalia monina*	Powdered Baron	Nymphalidae	OR	100	SR	PL	67
116	*Euthalia phemius*	White-edged Blue Baron	Nymphalidae	OR	150	SR	PL	75
117	*Herona marathus*	Pasha	Nymphalidae	OR	100	SR	DD	80
118	*Hestina nama*	Circe	Nymphalidae	OR	1000	SR	DD	100
119	*Hypolimnas bolina*	Great Eggfly	Nymphalidae	GL	600	SR	PL	90
120	*Hypolimnas misippus*	Danaid Eggfly	Nymphalidae	GL	300	SR	PL	77.5

121	*Issoria isaea*	Himalayan Queen Fritillary	Nymphalidae	PA	400	SR	MO	55
122	*Junonia atlites*	Grey Pansy	Nymphalidae	OR	100	SR	OL	60
123	*Junonia hierta*	Yellow Pansy	Nymphalidae	OR	300	SR	OL	52.5
124	*Junonia iphita*	Chocolate Pansy	Nymphalidae	OR	1350	SR	PL	67.5
125	*Junonia lemonias*	Lemon Pansy	Nymphalidae	OR	450	SR	PL	50
126	*Kallima inachus*	Orange Oakleaf	Nymphalidae	OR	1200	SR	PL	97.5
127	*Lebadea martha*	Knight	Nymphalidae	OR	100	SR	DD	68.5
128	*Lethe chandica*	Angled Red Forester	Nymphalidae	OR	100	SR	DD	70
129	*Lethe confusa*	Banded Treebrown	Nymphalidae	OR	1200	SR	OL	55
130	*Lethe dura*	Scarce Lilacfork	Nymphalidae	OR	100	SR	DD	77.5
131	*Lethe insana*	Common Forester	Nymphalidae	OR	400	SR	MO	57.5
132	*Lethe kansa*	Bamboo Forester	Nymphalidae	OR	100	SR	MO	70
133	*Lethe maitrya*	Barred Woodbrown	Nymphalidae	OR	800	SR	DD	50
134	*Lethe mekara*	Common Red Forester	Nymphalidae	OR	700	SR	OL	70
135	*Lethe nicetas*	Yellow Woodbrown	Nymphalidae	OR	100	SR	MO	51.5
136	*Lethe nicetella*	Small Woodbrown	Nymphalidae	OR	100	SR	DD	47

137	*Lethe siderea*	Scarce Woodbrown	Nymphalidae	OR	100	SR	DD	51.5
138	*Lethe sidonis*	Common Woodbrown	Nymphalidae	OR	1200	SR	MO	52.5
139	*Lethe sinorix*	Tailed Red Forester	Nymphalidae	OR	1600	LR	DD	74
140	*Lethe sura*	Lilacfork	Nymphalidae	OR	100	SR	MO	72.5
141	*Lethe verma*	Straight Banded Treebrown	Nymphalidae	OR	1600	LR	MO	57
142	*Melanitis leda*	Common Evening Brown	Nymphalidae	OR	1350	SR	OL	70
143	*Melanitis phedima*	Dark Evening Brown	Nymphalidae	OR	850	SR	OL	65
144	*Mimathyma ambica*	Indian Purple Emperor	Nymphalidae	OR	100	SR	MO	77.5
145	*Mimathyma chevana*	Sergeant Emperor	Nymphalidae	OR	100	SR	MO	77.5
146	*Moduza procris*	Commander	Nymphalidae	OR	150	SR	PL	67.5
147	*Mycalesis anaxias*	White-bar Bushbrown	Nymphalidae	OR	1000	SR	MO	51.5
148	*Mycalesis francisca*	Lilacine Bushbrown	Nymphalidae	OR	1200	SR	MO	51.5
149	*Mycalesis mestra*	White-edged Bush Brown	Nymphalidae	OR	100	SR	DD	45
150	*Mycalesis mineus*	Dark Branded Bush Brown	Nymphalidae	OR	1400	SR	OL	45

151	*Mycalesis perseus*	Common Bushbrown	Nymphalidae	OR	1350	SR	OL	46.5
152	*Mycalesis visala*	Long-branded Bushbrown	Nymphalidae	OR	100	SR	MO	50
153	*Neope pulaha*	Veined Labyrinth	Nymphalidae	OR	400	SR	DD	65
154	*Neope yama*	Dusky Labyrinth	Nymphalidae	OR	100	SR	DD	77.5
155	*Neorina hilda*	Yellow Owl	Nymphalidae	OR	100	SR	DD	62.5
156	*Neptis cartica*	Plain Sailer	Nymphalidae	OR	1350	SR	DD	57
157	*Neptis clinia*	Sullied Sailer	Nymphalidae	OR	1200	SR	PL	52.5
158	*Neptis hylas*	Common Sailer	Nymphalidae	OR	1200	SR	PL	55
159	*Neptis miah*	Small Yellow Sailer	Nymphalidae	OR	600	SR	DD	52.5
160	*Neptis narayana*	Broadstick Sailer	Nymphalidae	OR	200	SR	DD	65
161	*Neptis nashona*	Less Rich Sailer	Nymphalidae	OR	100	SR	DD	55
162	*Neptis nycteus*	Hockey Stick Sailer	Nymphalidae	OR	100	SR	DD	55
163	*Neptis pseudovikasi*	False Dingy Sailer	Nymphalidae	OR	100	SR	DD	62.5
164	*Neptis radha*	Great Yellow Sailer	Nymphalidae	OR	400	SR	DD	75
165	*Neptis sankara*	Broad Banded Sailer	Nymphalidae	OR	100	SR	DD	70
166	*Neptis sappho*	Rusty Sailer	Nymphalidae	PA	1350	SR	DD	50.5

167	*Neptis soma*	Creamy Sailer	Nymphalidae	OR	600	SR	MO	50.5
168	*Neptis zaida*	Pale Green Sailer	Nymphalidae	OR	100	SR	DD	70
169	*Orinoma damaris*	Tiger brown	Nymphalidae	OR	950	SR	MO	77
170	*Orsotriaena medus*	Medus Brown	Nymphalidae	OR	100	SR	OL	50
171	*Pantoporia hordonia*	Common Lascar	Nymphalidae	OR	1000	SR	OL	47
172	*Parantica aglea*	Glassy Tiger	Nymphalidae	OR	1550	LR	OL	77.5
173	*Parantica sita*	Chestnut Tiger	Nymphalidae	OR	1950	LR	OL	95
174	*Phalanta phalantha*	Common Leopard	Nymphalidae	OR	600	SR	PL	55
175	*Polyura dolon*	Stately Nawab	Nymphalidae	OR	100	SR	DD	*93*
176	*Pseudergolis wedah*	Tabby	Nymphalidae	OR	100	SR	MO	60
177	*Raphicera satricus*	Large Tawny Wall	Nymphalidae	OR	100	SR	DD	62.5
178	*Rohana paristas*	Black Prince	Nymphalidae	OR	150	SR	OL	47.5
179	*Rohana parvata*	Brown Prince	Nymphalidae	OR	100	SR	DD	55
180	*Stibochiona nicea*	Popinjay	Nymphalidae	OR	1750	LR	MO	70
181	*Sumalia daraxa*	Green Commodore	Nymphalidae	OR	400	SR	OL	65
182	*Symbrenthia brabira*	Himalayan Jester	Nymphalidae	OR	950	SR	OL	47.5

183	*Symbrenthia hypselis*	Spotted Jester	Nymphalidae	OR	650	SR	DD	47.5
184	*Symbrenthia lilaea*	Common Jester	Nymphalidae	OR	1000	SR	MO	50
185	*Symbrenthia niphanda*	Blue Tailed Jester	Nymphalidae	OR	550	SR	OL	55
186	*Tanaecia julii*	Common Earl	Nymphalidae	OR	600	SR	DD	75
187	*Heteropsis malsara*	White-line Bushbrown	Nymphalidae	-	850	SR	DD	45
188	*Tirumala septentrionis*	Dark Blue Tiger	Nymphalidae	OR	1550	LR	PL	85
189	*Vanessa cardui*	Painted Lady	Nymphalidae	GL	2450	LR	PL	62.5
190	*Vanessa indica*	Indian Red Admiral	Nymphalidae	GL	1950	LR	PL	60
191	*Vindula erota*	Cruiser	Nymphalidae	OR	150	SR	MO	91
192	*Ypthima huebneri*	Common Fouring	Nymphalidae	OR	850	SR	MO	36
193	*Ypthima sakra*	Himalayan Fivering	Nymphalidae	OR	950	SR	OL	50
194	*Yptima baldus*	Common Fivering	Nymphalidae	OR	1000	SR	OL	34
195	*Yptima newara*	Newara Threering	Nymphalidae	OR	100	SR	DD	47.5
196	*Atrophaneura varuna*	Common Batwing	Papilionidae	OR	100	SR	OL	112
197	*Byasa dasarada*	Great Windmill	Papilionidae	OR	1200	SR	MO	120
198	*Byasa polyeuctes*	Common Windmill	Papilionidae	OR	1200	SR	OL	125

199	*Graphium agamemnon*	Tailed Jay	Papilionidae	OR	800	SR	PL	92.5
200	*Graphium chironides*	Veined Jay	Papilionidae	OR	100	SR	OL	87.5
201	*Graphium colanthus*	Glassy Blue Bottle	Papilionidae	OR	100	SR	PL	88.5
202	*Graphium doson*	Common Jay	Papilionidae	OR	150	SR	PL	75
203	*Graphium eurypylus*	Great Jay	Papilionidae	OR	100	SR	PL	87.5
204	*Graphium sarpedon*	Common Blue Bottle	Papilionidae	OR	1000	SR	PL	85
205	*Pachliopta aristolochiae*	Common Rose	Papilionidae	OR	450	SR	OL	95
206	*Papilio alcmenor*	Red Breast	Papilionidae	GL	100	SR	DD	120
207	*Papilio arcturus*	Blue Peacock	Papilionidae	GL	100	SR	OL	120
208	*Papilio bianor*	Common Peacock	Papilionidae	GL	1200	SR	OL	110
209	*Papilio castor*	Common Raven	Papilionidae	GL	150	SR	OL	110
210	*Papilio clytia*	Common Mime	Papilionidae	GL	600	SR	OL	95
211	*Papilio helenus*	Red Helen	Papilionidae	GL	1750	LR	OL	120
212	*Papilio memnon*	Great Mormon	Papilionidae	GL	1750	LR	OL	135
213	*Papilio nephelus*	Yellow Helen	Papilionidae	GL	850	SR	OL	122.5
214	*Papilio paris*	Paris Peacock	Papilionidae	GL	800	SR	OL	115

215	*Papilio polymnestor*	Blue Mormon	Papilionidae	GL	100	SR	PL	135
216	*Papilio polytes*	Common Mormon	Papilionidae	GL	600	SR	OL	95
217	*Papilio protenor*	Spangle	Papilionidae	GL	1350	SR	OL	120
218	*Troides aeacus*	Golden Birdwing	Papilionidae	OR	400	SR	OL	153.5
219	*Troides helena*	Common Birdwing	Papilionidae	OR	650	SR	MO	155
220	*Appias albina*	Common Albatross	Pieridae	OR	100	SR	PL	70
221	*Appias indra*	Plain Puffin	Pieridae	OR	100	SR	PL	65
222	*Appias lalage*	Spot Puffin	Pieridae	OR	2000	LR	DD	67.5
223	*Appias lyncida*	Chocolate Albatross	Pieridae	OR	100	SR	PL	62.5
224	*Appias olferna*	Striped Albatross	Pieridae	OR	100	SR	OL	60
225	*Catopsilia pomona*	Common Emigrant	Pieridae	OR	100	SR	PL	67.5
226	*Catopsilia pyranthe*	Mottled Emigrant	Pieridae	OR	1350	SR	PL	67.5
227	*Cepora nadina*	Lesser Gull	Pieridae	OR	150	SR	MO	60
228	*Cepora nerissa*	Common Gull	Pieridae	OR	100	SR	OL	52.5
229	*Colias fieldii*	Dark Clouded Yellow	Pieridae	PA	800	SR	OL	52.5
230	*Delias agostina*	Yellow Jezebel	Pieridae	OR	850	SR	DD	71.5

231	*Delias belladonna*	Hill Jezebel	Pieridae	OR	750	SR	MO	89.5
232	*Delias descombesi*	Red Spot Jezebel	Pieridae	OR	450	SR	MO	77.5
233	*Delias eucharis*	Common Jezebel	Pieridae	OR	100	SR	PL	80
234	*Delias pasithoe*	Red Base Jezebel	Pieridae	OR	150	SR	MO	80
235	*Dercas verhuelli*	Tailed Sulphur	Pieridae	OR	650	SR	MO	55
236	*Eurema andersoni*	One Spot Grass Yellow	Pieridae	GL	450	SR	DD	41.5
237	*Eurema blanda*	Three Spot Grass Yellow	Pieridae	GL	1000	SR	OL	42.5
238	*Eurema brigitta*	Small Grass Yellow	Pieridae	GL	100	SR	OL	35
239	*Eurema hecabe*	Common Grass Yellow	Pieridae	GL	600	SR	OL	45
240	*Eurema laeta*	Spotless Grass Yellow	Pieridae	GL	100	SR	OL	37.5
241	*Gandaca harina*	Tree Yellow	Pieridae	OR	600	SR	DD	40
242	*Hebomoia glaucippe*	Great Orange Tip	Pieridae	OR	600	SR	OL	90
243	*Ixias pyrene*	Yellow Orange Tip	Pieridae	OR	600	SR	MO	60
244	*Leptosia nina*	Psyche	Pieridae	-	100	SR	PL	42.5
245	*Pieris brassicae*	Large Cabbage White	Pieridae	PA	600	SR	PL	70

246	*Pieris canidia*	Indian Cabbage White	Pieridae	PA	2550	LR	OL	52.5
247	*Prioneris thestylis*	Spotted Sawtooth	Pieridae	OR	100	SR	OL	80
248	*Abisara fylla*	Dark Judy	Riodinidae	OR	2000	LR	MO	55
249	*Dodona adonira*	Striped Punch	Riodinidae	OR	200	SR	MO	45
250	*Dodona dipoea*	Lesser Punch	Riodinidae	OR	400	SR	OL	40
251	*Dodona eugenes*	Tailed Punch	Riodinidae	OR	200	SR	MO	40
252	*Dodona ouida*	Mixed Punch	Riodinidae	OR	800	SR	MO	45
253	*Zemeros flegyas*	Punchinello	Riodinidae	OR	1750	LR	MO	37.5

Table A.2: The life-history traits of butterflies used in the study on butterflies of Rangeet Valley, Sikkim, eastern Himalaya.

Traits	Description	Data type
Range Size	Difference between highest and low elevation (meters)	Numeric
Biogeographic affinity	i) global (having center of diversity in two regions, ii) oriental (affinity to hot, humid, evergreen forest habitats) iii) palearctic (affinity to colder and temperate region) and iv) African species (having affinity to hot and drier habitats)	Categorical
Host plant specialization	i) monophagous (larva feeding on plants in only one genus), ii) oligophagous (larva feeding on plants in single family, but more than one genus), and iii) polyphagous species (larva feeding on plants in more than one families and orders)	Categorical
Wingspan	Mean wingspan (mm)	Numeric

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SHORT COMMUNICATION

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A NEW RECORD OF THE LESSER-KNOWN BUTTERFLY SMALL WOODBROWN *LETHE NICETELLA* DE NICÉVILLE, 1887 (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE) FROM KHANGCHENDZONGA NATIONAL PARK, SIKKIM, INDIA

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Abstract: This study reports the recent sighting of Small Woodbrown *Lethe nicetella* from Khangchendzonga National Park in West Sikkim District, India. It was originally described by de Nicéville (1887) based on the collection of males and one female by Otto Möller from Sikkim but the exact type locality was unknown. We also reviewed various historical and contemporary reports on the description and distribution of this species. We did not find any report of collection or sighting of the species from India after Elwes & Möller (1888). The occurrence of this species in Sikkim is mentioned in Haribal (1992) but it is not clear whether the report is based on sightings or historical records because sighting location is not given, indicating its description based on museum specimens. Hence, we conclude that the Small Woodbrown *L. nicetella* was sighted after a gap of around 120 years. Further, we have provided the first photographic records of a live individual of this species from India. Our finding indicates a possibility of existence of many cryptic taxa that should be explored using morphological and molecular approaches.

Keywords: Butterflies, *Lethe nicetella*, Sikkim, Small Woodbrown.

Lethe Hubner [1819], is a butterfly genus under the subfamily Satyrinae of the family Nymphalidae. The genus is distributed from Borneo through the Sunda Islands, Japan, Siberia, Himalaya and peninsular India (Mani 1986). Morphologically, the upperpart of these butterflies are brown with apical spots on the forewing and spots or ocelli on the hindwing. They also bear distinctive ocelli on the under parts of the wings. The habitat of most of the species of this genus is bamboo forest or grassy patches in the forest.

Sikkim is a small land locked Himalayan state in India covering an area of 7,096km². It lies in western extremities of the eastern Himalaya, a part of one among the 36 biodiversity hotspots of the world (CEPF

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Full length article

Kitam Bird Sanctuary, the only low elevation protected area of Sikkim: A conservation hotspot for butterflies in the Eastern Himalaya

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ABSTRACT

The lowland areas of the Himalayan region are subjected to immense anthropogenic pressure because of least representation in the protected area network. Kitam Bird Sanctuary is the only representative protected area that occurs below 1000 m in Sikkim state of India (a part of globally significant biodiversity hotspot of Himalayas) and serves as the refuge for various species of flora and fauna. Here we studied butterfly diversity and community composition in Kitam Bird Sanctuary (a small protected area of 6 km^2 geographical area) following point count method spread across predetermined transects. Altogether 1674 butterflies belonging to 111 species and six families were recorded after completion of 240 point counts. Among these, 18 species are federally protected under the Wildlife (Protection) Act (1972) of India. Most of the butterflies were forest specialist in terms of habitat preference, whereas based on host plant specificity, the butterfly community was mostly dominated by generalist feeder (Oligophagous II and Polyphagous). Butterfly community parameters showed a strong correlation with habitat variables. While Kitam Bird Sanctuary is primarily designated for conservation of lowland birds, the high diversity of butterflies both in terms of taxonomic richness and trait composition suggests that the sanctuary harbors an ideal habitat for butterflies of the tropical region and invites conservation attention.

Introduction

Habitat loss remains the greatest threat to biodiversity, especially in tropical regions (Laurance, 1999; Brooks et al., 2002; Primack, 2014). The loss and degradation of habitat have been identified as the main threat to 85% of IUCN Red List species (IUCN, 2015). Butterflies are highly sensitive to alteration in habitat structure due to their exclusive dependency and specificity to plants, both as larval host as well as nectars (Kremen, 1992; Blair and Launer, 1997). Increasing land use intensities leading to degradation and fragmentation of habitats causes a decline in the diversity of butterflies (Schulze et al., 2004; Posa and Sodhi, 2006; Francesconi et al., 2013).

Biodiversity conservation measures around the globe have been focused mainly on the establishment of protected areas (Burner et al., 2001). Studies have shown that protected areas are rich in biodiversity, including butterflies, as compared to unprotected forests (Akwashiki et al., 2007; Chinaru and Joseph, 2011; Klorvuttimontara et al., 2011). The occurrence of complex vegetation structure which creates an array of micro-habitats has been attributed to the high diversity of butterflies in protected areas (Orimaye et al., 2016). Butterflies complementarily are a good indicator of forest health and serves as the surrogate taxa for biodiversity wealth (Bhardwaj et al., 2012; Hayes et al., 2009). Hence, assessment of butterfly diversity serves as a basis for evaluating the status of protected areas (Majumder et al., 2012).

Besides taxonomic composition based indices (e.g species richness and Shannon-Weiner diversity), life history traits are used to measure biodiversity in recent years (Slancarova et al., 2016; Lee and Martin, 2017). Traits strongly influence functioning of a species in an ecosystem and reflects how species respond to environmental conditions (Petchey and Gaston, 2002; Dreiss et al., 2015; Aguirre-Gutiérrez et al., 2017). In case of lepidopterans, difference in life history traits such as host plant association and habitat specialization are responsible for differential sensitivities to habitat loss (Summerville and Crist, 2004; Soga and Koike, 2012). Generalist species increases with the land use intensification, whereas specialist group displays the opposite trend (Börschig et al., 2013; Kitahara et al., 2000).

The Himalayan state of Sikkim, located in the Eastern Himalayan mountain in India, consists of around 689 species of butterflies representing approximately 50% species found in the Indian sub-continent (Haribal, 1992; Kehimkar, 2016). The continuous gradation of climate and changes in vegetation structure due to a steep rise in elevation offers a unique habitat for the existence of wide diversity of butterflies in the region. The lowland tropical valleys in Sikkim, especially below 1000 m, have been considered as hotspot for butterflies

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RESEARCH ARTICLE

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Do sub-groups of butterflies display different elevational distribution patterns in the Eastern Himalaya, India?

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Abstract

Understanding the pattern of biodiversity along environmental gradients helps in identifying diversity hotspot areas that can be prioritized for conservation. While the elevational distribution of several taxa has been studied, responses of the sub-groups within a taxon to elevation and its associated factors are not properly understood. Here we study species richness and butterfly density along an elevation gradient in Sikkim, Eastern Himalaya, India and explore the underlying causes of the patterns. We sampled butterflies using a fixed-width point count method in 16 elevational bands (150–200 m intervals), between a range of 300 and 3300 m a.s.l. We categorized butterflies into various sub-groups based on family, range size, biogeographic affinity, and host-plant specialization. We recorded 3603 individuals and 253 species of butterflies after the completion of 1860 point counts. Overall, species richness in the majority of the sub-groups (except for Riodinidae and Palearctic species) declines with elevation, as does the density of almost all the sub-groups. From a selection of environmental factors, annual actual evapotranspiration has the strongest effect on the species richness pattern of butterflies as well as on the density of the overall butterfly community, especially the Lycaenidae family. The richness and density of butterfly groups display varied responses to the richness and density of trees and shrubs. The conducive climatic conditions and diverse habitats in the lower valleys of the Eastern Himalaya support a high diversity of butterflies (with majority of small range species) and thus warrants conservation attention.

Highlights

- The distribution of biodiversity along mountain elevational gradients has been well studied, but the disparity in patterns between various organisms and associated factors makes it difficult to develop a universal model for explaining the variation of biodiversity.
- We report elevational patterns of species richness and density of butterflies in the Eastern Himalaya, both at whole group and sub-group levels.
- A general decline in species richness and density with elevation is not supported for Riodinidae and for Palearctic species.
- A measure of water energy balance, annual actual evapotranspiration, is the best correlated variable with species richness trends in butterflies.
- Our paper highlights the importance of low elevation forests for butterfly diversity in the Eastern Himalaya.

Keywords: Biodiversity pattern, biogeographic affinity, butterflies, elevational gradient, environmental factors, Himalaya, spatial factors.

Introduction

There has been an upsurge in studies assessing biodiversity patterns across broad spatial scales, explaining the underlying processes, and exploring any conservation implications (Stevens 1992, Sánchez-Rodríguez and Baz 1995, Rahbek 2005, Acharya et al. 2011a, Wu et al. 2013a, Li and Feng 2015, Rana et al. 2019, Supriya et al. 2019). These studies may serve as a baseline for understanding the response of biological assemblages to climate change (Hodkinson 2005). Additionally, environmental gradient studies

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