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The composition and phenology of butterflies are determined by their functional trait in Indian tropical dry forests

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Abstract

To understand the effects of local landscape factors on functional species composition and phenology of butterflies across multiple spatial scales, a study was carried out in a tropical dry forest of the northern highlands of the Eastern Ghats of India from November 2016 to October 2017. A total of 3343 individuals of 88 species of butterflies were recorded, under 62 genera, 18 subfamilies, and six families in three different forest types (open, riparian, dense). Butterfly species richness showed no significant deviations, but diversity patterns varied across transects. Beta diversity indicated differences in common species populations, likely due to uneven resource distribution in study site forests. The contribution of β transect to gamma diversity was greater than that of β elevation, except for specialists. Specialists were favoured by landscape attributes over forest type. Butterfly abundance peaks in April for open and dense forests and May for riparian forests. Results show variation in seasonal patterns across different forest types (F = 15.92, P < 0.001). Generalists and versatilists are more prevalent in April and February, while specialists are more abundant from October to November. Relative humidity, shrub density, and temperature were the major contributors (40.2%) for richness, whereas relative humidity and shrub density contributed 26.3% for abundance. The relative humidity was predominant over temperature for species richness and is a major predictor for assemblages of generalist species. Elevation-dependent resource utilization is crucial for habitat specialists, underscoring the significance of spatial elevation zones in effective conservation planning strategies.

Keywords Eastern Ghats · Koraput · Lepidoptera · Additive partitioning framework · Landscape · Microenvironment

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Introduction

Forests and woodlands act as biodiversity reservoirs for over 80% of terrestrial biodiversity (Aerts and Honnay 2011), and primary forests in the tropics host the greatest biodiversity, with at least two-thirds of the world's organisms (Raven 1988). Tropical forests, with their exceptional local diversity, endemism, species turnover along gradients, and high genetic divergence, stand out as the most diverse biome (Dirzo and Raven 2003; Watson et al. 2019). In addition, the largest primary production and evapotranspiration in the tropics makes them a globally important ecosystem for regulating global climate (Malhi 2012). Butterflies are highly sensitive to habitat disturbance and climate change, making them widely studied indicator species and are easy to monitor or assess (Pollard and Yates 1993; Fleishman and Murphy 2009). In the past four decades, there has been a 35% reduction in the global abundance of Lepidoptera (butterflies and moths), as indicated by a recent study (Dirzo et al. 2014). This decline is linked to the expansion of arable land, deforestation, and the effects of global warming (Sánchez-Bayo and Wyckhuys 2019). The high butterfly endemism in the tropics is crucial for understanding ecology amid habitat destruction and climate change (Lewis and Senior 2011). Vegetation influences butterfly assemblages by offering a stable, humid, cooler, and low-light habitat compared to the surrounding landscape (Sutton and Collins 1991; Swengel 1998). Co-evolved with plants, the butterfly acts as a pollinator and an herbivore in the terrestrial ecosystem (Ehrlich and Raven 1964; Bawa 1990). Resource-based habitat use in different stages of the life cycle as consumables (e.g., host plant parts, nectar) and utilization of sites (e.g., roost sites, mate location sites, pupation sites) and the interaction with the environment from the functional viewpoint is the major concern in butterfly ecology (Dennis et al. 2006; Cˇelik et al. 2015). The functional group (i.e., Generalist, Versatilist and Specialist) and their composition quantify the various processes within a community, crucial for shaping its structure and maintaining dynamic stability (Chen et al. 2011; Zografou et al. 2020). The definition of functional groups is based on their utilization of a range of prey types or their ability to thrive in various environmental conditions (Richmond et al. 2005). The generalist–specialist spectrum in butterflies is used to understand landscape changes, patch connectiveness, and matrix quality (Dennis 2010; Brito et al. 2014). The diversity and distribution of functional groups are heterogeneously distributed in various spatial and temporal scales (de Vries and Walla 1999). Different spatial and temporal scales can create variations in the structure of the food web, resource use, dispersal ability, habitat connectivity, and climate factors which modulate the functional diversity (Montoya et al. 2015; Mahon et al. 2023). Elevation creates higher spatial and temporal community shifts due to its high topographic heterogeneity and plays a crucial role in specialist species conservation (Habel et al. 2021). Furthermore, forest types i.e., open, riparian, and dense forest create preferred microenvironments for functional traits of butterflies. Riparian forests, with relatively moderate daytime temperatures and heterogeneous vegetation, were the most preferred microhabitat for specialists, followed by disturbance-prone open forests and homogeneous dense forests (Mahata et al. 2023). Specialists dominate limited resources in isolated and undisturbed habitats, while generalists benefit from any resource and may migrate readily between appropriate patches. The versatilists are the most severely impacted by recent environmental changes since they cannot compete with any of these alternative strategies (Dapporto and Dennis 2013). In addition, specialist species appear to be more significantly impacted by habitat fragmentation, with recent studies (Ries and Debinski 2001; Soga and Koike 2013) suggesting that they exhibit lower emigration rates from fragmented habitats compared to generalist

species. Furthermore, specialist species demonstrate reduced resistance and resilience capacity in the face of habitat degradation when compared to habitat generalists (Cleary and Genner 2004). Therefore, in comprehending the community structure and population dynamics of butterflies within a specific landscape, the crucial factors lie in understanding their ecological traits and how they interact with the environment (Sonnay et al. 2014).

Many studies have demonstrated the change in butterfly population dynamics in response to climatic factors. Butterfly assemblages have a positive association with temperature and sunshine (Pollard and Yates 1993; Roy et al. 2001) and a negative association with higher precipitation and wind speed (Pollard 1988; Stefanescu et al. 2003; Cormont et al. 2011). Weather impacts not only fluctuations in butterfly abundance but also influences the timing of the flight period, the number of generations in a particular season, and the dispersal and colonization of new sites (Pollard and Yates 1993). Warm dry summers, along with high rainfall in the early months of the previous year and late spring frost, are beneficial for the butterfly flight period (Pollard and Yates 1993). In recent years, global climate change has not only altered the geographical distribution of species but also affected their assemblages, life history strategies, and phenology (Kharouba et al. 2014). The significance of phenology has grown as an indicator of how species respond to environmental shifts, climatic variations, and global changes (Roy and Sparks 2000). Phenology refers to the timing of cyclical or seasonal biological events, including budburst, flowering, leaf fall, seed set, and dispersal, in plants, as well as egg laying, eclosion, pupation, hibernation, flight period, and migration in insects (Warren et al. 2021). Alterations in the phenology of host plants can lead to corresponding changes in the flight period and utilization of host plants by butterflies over time and space (Wiklund and Friberg 2014; Navarro-Cano et al. 2015). Phenological changes in butterflies, driven by rising temperatures, were linked to ecological traits. Multivoltine species consistently extended flight periods, while univoltine species were less consistent. Polyphagous species advanced and extended flights, while oligophagous species slowed and shortened flights in warmer temperatures (Zografou et al. 2021). Thus, species-specific ecological traits (larval trophic specialization, larval diet composition, voltinism) and local climatic variables (temperature, aridity, and growing degree days) shape butterfly phenological responses to climate change and are linked to important community impacts (Zografou et al. 2021). In a study conducted by de Arce Crespo and Gutiérrez (2011) on butterflies in central Spain, it was found that increase of 1 °C temperature could result in the emergence of butterflies 3.7 days earlier for entire groups and ranging from 2.6 to 8.2 days earlier for certain univoltine species. For British butterflies, Roy and Sparks (2000) have noted a correlation where the mean emergence date may increase by 2 to 10 days for each degree Celsius rise in temperature. Furthermore, temporal variation in butterfly fauna along with host plants is an essential phenomenon required for coevolution, pollination, and subsequently food production in fruit trees (Myers et al. 2017; Ramírez and Kallarackal 2018).

India is one the mega-diverse countries of the world and contributes 7–8% of world species composition, with tropical forests expanding more than 73% of its terrestrial ecosystem has high endemism (MoEF 2014). In the last eight decades, forest cover in India has been reduced by up to 28% (Sudhakar Reddy et al. 2016) and subsequently caused severe declines in biodiversity (Mehdi 2010; Barlow et al. 2016). Depletion of forest cover along with biodiversity loss in the Eastern Ghats have been increasingly reported (Reddy et al. 2013; Adhikary et al. 2019), and subsequent conservation efforts have been implemented (Rawat 1997; Balaguru et al. 2006). Butterfly biology studies in India started over two and half centuries ago but have faced challenges in progressing at a comparable pace (Kunte 2000; Kunte et al. 2020). In India, butterfly studies mainly focus on traditional

morpho-taxonomy, particularly in hotspot regions (MoEF 2014; Kunte et al. 2020). However, very few studies mainly focused on butterfly ecology, phenology, behaviour, and evolutionary biology (Wynter-Blyth 1957; Kunte 2000; Bhaumik and Kunte 2018). This gap underscores the necessity for greater attention and research focus in the aforementioned areas of study (Kunte et al. 2020). Community-based population and ecological studies of butterfly fauna have increased in recent years in India. Kunte (1997) studied the seasonal pattern of butterfly fauna of tropical habitats in the northern Western Ghats of India with special attention on herbivory. The diversity of butterflies in the Himalayan region is predominantly influenced by the elevational gradient (Bhardwaj et al. 2012; Acharya and Vijayan 2015). Additionally, studies on urban landscapes emphasize the significance of microclimate (Gupta et al. 2019), and anthropocentric values play a role (Mukherjee et al. 2015).

The Eastern Ghats of India, a region rich in biodiversity, provide immense opportunities for understanding butterfly populations in tropical dry forests (Mahata et al. 2023). The Eastern Ghats which is undergoing rapid anthropogenic transformation (Ramachandran et al. 2018), harbour several patches of primary forest, play important repositories for species conservation, and are most useful to understanding the functional role of ecological traits. Several butterfly diversity studies (Sethy et al. 2007; Prasanna Kumar et al. 2011; Bubesh Guptha et al. 2014; Mahata et al. 2019a, b) cover the Eastern Ghats, yet phenological and autecological details remain unexplored in this region. To address the existing knowledge gap concerning the spatial and temporal distribution linked to the functional traits of butterflies, this research endeavours to achieve the following objectives: (1) comprehend the spatial distribution of butterflies with their functional traits, (2) gain insights into the phenology of butterflies based on their functional traits, and (3) explore the influence of microenvironmental variables on functional traits. To understand the above objectives, this study focuses on examining the functional traits of butterflies to landscape attributes and microenvironmental factors in the tropical dry forests of Koraput of southern Odisha in the Eastern Ghats of India. The hypotheses of the study are: (1) Functional diversity arises randomly as butterflies distribute across various spatial scales; (2) Functional groups of butterflies showed different seasonal flight activity patterns in response to their different microenvironment requirements at different spatial scales; and (3) Richness and abundance of functional groups of butterflies are influenced differently by different microenvironmental variables.

Materials and methods

Study area

This study was carried out in the primary tropical dry forest of Koraput district (18° 14′ to 19° 13′ N latitude and 82° 5′ to 83° 25′ E longitude) of southern Odisha of India (Fig. 1). The study area is covered with discontinuous hill ranges of northern Eastern Ghats with varying elevation ranges from 123 to 1655 m above mean sea level (Adhikary et al. 2019). Dry deciduous and moist deciduous tropical forests (Champion and Seth 1968) are the major forest types in this region, dominated by *Shorea robusta*, in association with *Pterocarpus marsupium, Anogeissus latifolia, Adina cordifolia, Tectona grandis, Mitragyna parvifolia, Terminalia arjuna, Terminalia bellirica, Terminalia chebula, Terminalia tomentosa, Dalbergia latifolia, Gmelina arborea, Xylia xylocarpa, Schleichera oleosa. Syzygium*
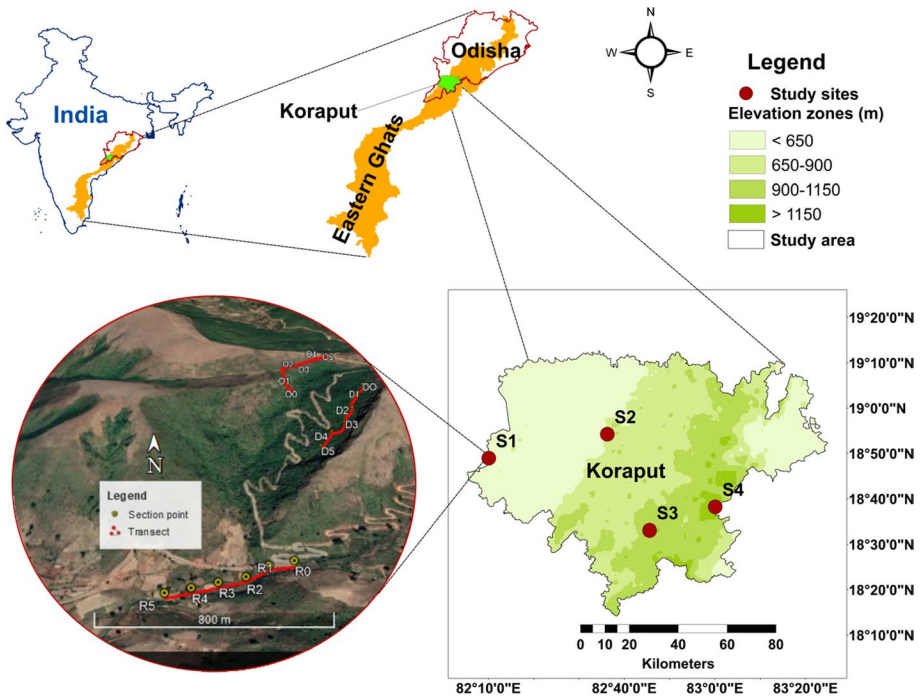
Fig. 1 Map illustrating the study area and its corresponding study sites (S1, S2, S3 and S4) organized along an elevation gradient. Each study site is delineated by three transects (highlighted in red), and each transect comprises five sections (depicted by yellow points, each prefixed with the forest type abbreviation: O open forest, R riparian forest, and D dense forest)

cumini, Diospyros melanoxylon, Boswellia serrata, Albizia species, Salmalia malabarica, Butea monosperma, etc. (FSI 1989). Recent agricultural expansions fragmented and transformed primary forests into secondary or degraded fragments, leading to increased open and scrub forests (Adhikary et al. 2019). The region experiences distinct dry (October to May) and wet seasons (June to September). The climate is seasonal and moderately humid, with temperature ranges from a minimum of 12 °C to a maximum of 38 °C (Mahata et al. 2019b) and 1452.2 mm in about 77 rainy days in a year (Adhikary et al. 2015). Nearly 81% of the annual rainfall occurs during monsoon by southwest monsoon (Adhikary et al. 2015). Undulating landscapes with heterogeneous vegetation and seasonal warmer and cooler climates make it a biodiversity-rich and endemic region (Majumdar 1988; Misra et al. 2009; Mahata et al. 2019b; FAO 2020).

Sampling design

Four sampling sites have been chosen based on elevational gradient (400–650 m, 650–900 m, 900–1150 m, and 1150–1400 m) and local protection categories (RF-Reserve Forest and PRF-Proposed Reserved Forest) (Fig. 1). Two of study sites are under reserve forest (S1-Dongrakhol RF: 18° 48′ 55.26″ N 82° 10′ 3.57″ E, elevation 420 m, area 54.58 km^2, and S2-Kondamali RF: 18° 54′ 13.68″ N 82° 36′ 14.07″ E, elevation 703.30 m, area 8.79 km^2) and two are under Proposed Reserve Forest (S3-Nandapur PRF: 18° 33′

1.90″ N 82° 45′ 34.27″ E, elevation 1001.87 m, area 533 km^2 and S4-Galigabeda PRF, 18° 38′ 15.39″ N 83° 0′ 20.01″ E, elevation 1062 m, area 1563 km^2). Each site encompassed heterogeneous forest, including Moist Peninsular High-Level Sal (S1), Dry Peninsular Sal Forest (S2), Southern Dry Mixed Deciduous Forests (S3), and Dry Savannah Forest (S4). Furthermore, each site was categorised into three major forest habitats: (1) Open Forest (OF), a forest with less than 35% canopy cover; (2) Riparian Forest (RF), a forest associated with a stream; (3) Dense Forest (DF), forest more than 35% forest cover. One 500 m transect was placed in each forest habitat i.e., OF, RF, DF in each study site. The mean distance between transects in each site was 1.5 ± 0.25 km and the mean distance among study sites was 39 ± 8.64 km, so each transect represented an independent sample (Zografou et al. 2017).

Butterfly sampling

A total of 12 transects i.e., 4 sampling sites × 3 transects (one 500 m transect in each of the three forest habitats) were monitored once each month from November 2016 to October 2017. Pollard transect recording (Pollard 1977) was adopted with modification for butterfly abundance count. Butterflies were counted inside an imagined box of 2.5 m on either side of the path and 5 m in front and above the observer from 0900 to 1300 h with a consistent pace of 60 min for each 500 m transect. All surveys were carried out using two observers, one to look for butterflies and the other to record data. Visual encounters, along with photographs, were adopted for species identification. Butterfly field guides (Wynter-Blyth 1957; Kunte 2000; Kehimkar 2008) were used for butterfly identification, and taxonomy was followed after Varshney and Smetacek (2015).

Functional groups

Functional relationships in an ecosystem mostly depend on habitat specialization and species assemblage. Habitat specialization was defined using a measure based on the host specificity index (*Sm*) followed after Novotny and Basset (1998). *Sm* measures the variation in butterfly abundance among habitats and acts as an indirect approach to specificity measurement. It is used to identify the functional group based on habitat preference. The index was calculated as:

$$Sm = \frac{\text{Number of individuals on the prefered habitat}}{\text{Total number of individuals}}$$

Based on *Sm* index, the forest butterflies were grouped into three categories: (1) habitat specialist: species exclusive in specific habitat (*Sm* ≥ 0.9), (2) habitat versatilist: species with habitat preferences (0.5 < *Sm* < 0.9), and habitat generalist: species which occurs in all habitats (*Sm* ≤ 0.5) (Brito et al. 2014).

Habitat characterization and measurement

Tree density (TD), Shrub density (ShD), Herb density (HD), and Canopy cover (CC) have been recorded once a month in each 100 m section of each 500 m transect on the same butterfly counting day. TD is quantified as the number of trees (10 cm diameter at 1.37 m height with barks) in a 5 m circular plot in each section point. In each tree plot, numbers

of shrubs (plants with < 3 m height and woody stem) and herbs (plants with soft stem and height < 1 m) have been counted for ShD and HD in one 2.5 m circular plot and two 1 m circular plot respectively (FSI 2002). TD and ShD data were converted into the number of plants per hectare (plants/ha) and HD into the number of herbs per square meter (herbs/m^2). Mean CC has been recorded in each section point in four directions (North, East, West, South) using GLAMA (Gap Light Analysis Mobile App. Version 3.0, Masaryk University, Brno, Czech Republic) application in a smartphone with a 16-megapixel inbuilt camera at the breast height (Tichý 2016; Mahata et al. 2019b).

Mean daily aerial temperature (Temp), relative humidity (RH), relative light intensity (LI), and wind speed (WS) have been measured in each section of the transect during butterfly count. Temp, RH, and WS were measured using a digital anemometer (AVM-06, HTC, India), and LI was measured using a digital light meter (LX-103, Lutron, India) at each section during transect count (Mahata et al. 2019a).

Data analysis

Sampling effort

To assess the sampling adequacy in this study, a sample-based rarefaction/extrapolation curve has been constructed (three times of the reference samples with 1000 times randomization) for each sampling site (Colwell et al. 2004) that relates visually the number of samples (transects) to the accumulative number of species i.e., species richness (S) using EstimateS 9.1.0 software (Colwell and Elsensohn 2014).

Diversity measurement

Species richness (S) and relative abundance (RA) are simple, quantitative measures, and have been widely used to define the biological diversity of a community. The number of species occurring within the community is referred to as species richness. The relative abundance is defined as the percentage of each species contributed to the total number of individuals of all species (Magurran 2004). In addition, an additive partitioning framework has been used in this study to test the null hypothesis that butterfly diversity is uniform in all spatial scales i.e., transects, forest types, and elevation-based study sites (Zografou et al. 2017).

The additive partitioning framework is a statistical approach in which the total species diversity in a region (γ) could be partitioned into additive components representing within-community diversity (α) and among-community diversity (β), where diversity is measured as species richness (S), or by using Shannon–Wiener index [$H' = \Sigma\ p_i\ \ln\ (p_i)$] where p_i is the proportional abundance of species i for i = 1 to n total number of species in the sample (Lande 1996). Because it allows for a direct comparison of α and β diversities, the additive partitioning framework is commonly used in testing ecological theory concerned with the determinants of species diversity at multiple spatial scales (Veech et al. 2002). The pooled data from all sampled months were aggregated by three spatial scales, i.e., transects (144 sampling units), forest types (12 sampling units), and elevation-based study sites (landscape level, four sampling units), to access the species diversity. Alpha (α) diversity was calculated as the average diversity at each scale, while beta diversity (β) was expressed as the difference between these levels (Lande 1996). The partition has been applied to all hierarchical spatial scales (transects, forest types, and elevation-based study sites) so that

the samples in lower hierarchical levels are nested within higher-level units (e.g., transects are nested within forest types and forest types are nested within the elevation-based study sites) (Table 1). α diversity at a given scale is the sum of the α and β diversity at the next lowest scale (i.e., $\alpha2 = \alpha1 + \beta1$ or $\beta1 = \alpha2 - \alpha1$). Total diversity (γ) was partitioned into α-diversity (i.e., average diversity of each transect) and β-diversity (i.e., species diversity among selected forest types and elevation-based study sites). Thus, the β-diversity component can be calculated as, $\beta = \gamma - \alpha$. The alpha diversity of the transects scale (α_{transect}) is the diversity of each transect. β_{transect} measures species diversity variation among transects in each forest, $\beta_{\text{forest types}}$ gauge diversity variation among different forest types within an elevation-based site, and $\beta_{\text{elevation}}$ assesses diversity variation among elevation-based study sites (Table 1).

These β components of this additive partitioning framework can be calculated using the following equations:

$$\beta_{\text{transect}} = \alpha_{\text{forest type}} - \alpha_{\text{transect}}$$

$$\beta_{\text{forest type}} = \alpha_{\text{elevation}} - \alpha_{\text{forest type}}$$

$$\beta_{\text{elevation}} = \gamma - \alpha_{\text{elevation}}$$

Therefore, γ- diversity was derived from the above equations in this study followed by Veech and Crist (2009):

$$\gamma = \alpha_{\text{transect}} + \beta_{\text{transect}} + \beta_{\text{forest type}} + \beta_{\text{elevation}}$$

Analyses of diversity were performed using PARTITION software (version 3.0), where alpha and beta estimates were tested through a randomization procedure at 5% level of significance (Veech and Crist 2009).

Butterfly phenology analysis

A monthly monitoring system led to an understanding of the phenology based on circular statistics. The peak abundance dates of butterflies have been converted to angles from 0° to 300° for January to October 2017 and 300° to 360° for November and December 2016; the interval for each month is 30° (Morellato et al. 2010; Brito et al. 2014). This study used the mean vector (μ) to describe the central tendency, which was later converted into mean date (Zar 2014). The angular deviation (s) used to measure the dispersion of a set of angles around their mean angle of directional data, followed by Zar (2014). The significant seasonal pattern among habitats and functional groups was tested with the Rayleigh test, and the degree of seasonality in the peaks of abundance of total butterfly assemblages was tested with Watson-Williams multi-sample test (Watson and Williams 1956; Zar 2014) at 5% level of significance. Circular statistics have been performed using NCCS (version 12.0.2) software (NCSS 2018).

Effect of ecosystem parameters on butterflies

The mean and standard deviation (i.e., mean ± SD) of abiotic parameters (Temp, RH, LI, and WS) and vegetation variables (CC, TD, ShD, and HD) were analysed based on forest types and elevation gradients. The multiple linear regression (MLR) model has been tested

Table 1 Hierarchical model of species diversity studies of butterflies in Koraput of southern Odisha, Eastern Ghats of India

Landscape level	α diversity	β diversity
Tropical dry forests of Koraput	Additive species diversity of the tropical dry forests of Koraput	Variation in species diversity Among elevation-based study sites, forest types and transects ($\beta_{elevation}$)
Elevations	Species diversity of each elevation-based study site ($\alpha_{elevation}$)	Variation in species diversity among forest types and transects ($\beta_{forest\ type}$)
Forest types	Species diversity of each forest type ($\alpha_{forest\ type}$)	Variation in species diversity among transects ($\beta_{transect}$)
Transects	Species diversity of each transect ($\alpha_{transect}$)	

to understand the effects of ecosystem parameters on butterflies. The model selection was based on the step-wise regression method and tested a 5% significance level. Multicollinearities among variables have been tested with bivariate correlations of a cut-off value of 0.70, and a common cut-off threshold is a tolerance value of 0.20 (Hair et al. 2019). The most significant variable with the least correlated to each other was considered for modelling (Hair et al. 2019). The model was performed with SPSS Statistics version 23 (IBM Corporation, USA).

Results

Status and distribution of butterflies

A total of 3343 individual butterflies of 88 species were recorded under 62 genera, 18 subfamilies, and six families (Table S1). Nymphalidae was the family with the highest number of species (33), followed by Lycaenidae (18), Pieridae (14), and both Hesperiidae and Papilionidae with 11 species each. Riodinidae had the lowest number of species, with only one. Abundance showed different patterns, with maximum individuals by Nymphalidae (1564), followed by Pieridae (1040), Lycaenidae (432), Papilionidae (235), Hesperiidae (66), and Riodinidae (6). Among 88 species, 50 are versatilists found in more than one habitat, 23 are generalists found in all habitats and 15 are specialists in a particular habitat. Out of 50 versatilist butterfly species, the maximum species were found under Nymphalidae (20), followed by Lycaenidae (10), Pieridae (9), Papilionidae (8), and Hesperiidae (3). The Nymphalidae family has the highest generalist species (8), followed by Lycaenidae (5), Hesperiidae (4), Papilionidae (3), Pieridae (2), and Riodinidae (1). Out of 15 specialist species, maximum was under Nymphalidae (5), followed by Hesperiidae (4), and least by both Lycaenidae (3) and Papilionidae (3). Among forest types, RF showed maximum species richness (76), followed by OF (74), and the least by DF (48). Similar trends were also found in the abundance of butterflies in this study. Maximum abundance was observed in RF (1449 individuals), followed by OF (1362), and least by DF (532). *Eurema hecabe* was the most dominant species in this study contributing 15.73% of the total butterfly assemblages. Based on forest types, *Eurema hecabe* was the most dominant species in OF (RA = 21.15%) whereas *Euploea core* was the most dominant species in both riparian forests (RA = 12.49%) and DF (RA = 12.97%) (Table S1). Overall sampling completeness

was sufficient, close to 90% or above for all habitats and it was also supported by a sample-based rarefaction/extrapolation curve approaching asymptote (Fig. 2). Furthermore, the sample-based rarefaction/extrapolation curve showed OF demonstrated the highest level of sample completeness followed by DF, as evidenced by the rarefaction/extrapolation curve approaching a horizontal asymptote after an initial rise. This suggests that the observed species count did not increase significantly beyond the initial phase. In contrast, the RF exhibited continuous growth beyond the early stage, implying that additional survey locations are likely to yield the discovery of new species (Fig. 2).

Diversity measurements and seasonal flight patterns of butterfly groups

The highest β component (β_elevation) in this additive partitioning framework was always greater than expected by chance for both diversity measures (Table 2). However, the most noticeable result was that the β_transect had a considerably larger contribution to the total gamma diversity compared to the β_elevation (Table 2, Fig. 3). However, in the specialist group, β_elevation had a higher contribution to the total γ diversity. Except for the generalist group, β_transect did not show any significant difference in species richness compared to what was expected by chance. In addition, the α component showed similar results for both diversity measures. For the Shannon–Wiener index (H′), all three of β diversity values were significantly higher (p < 0.05) than those expected by chance (Table 2).

Different temporal variations of different groups of butterflies have been recorded in the study period (Table S1). A total of 12 species showed year-round occurrence, i.e., *Ariadne ariadne*, *Junonia iphita*, *Melanitis leda, Jamides celeno, Euploea core, Phalanta phalantha, Tanaecia lepidea, Junonia lemonias, Mycalesis perseus, Papilio demoleus, Papilio polytes, Eurema hecabe* and seven species: *Sarangesa dasahara, Catochryspos strabo, Talicada nyseus, Tirumala septentrionis, Eurema laeta, Moduza procris, Cepora nerissa* having restricted flight period of less than a month (Table S1). The mean vector (μ) (which indicates the mean flight date) of the total sampled assemblage for each habitat ranged from March to April (Table 3). Peaks of butterfly abundance in OF and DF occurred in April, while the higher abundance in the RF was recorded in May (Fig. 4a). Based on the Watson–Williams multi-sampling test, the seasonal variation in butterfly abundance peaks differed among forest types (F = 15.92, p < 0.001). All functional groups (generalists, specialists, and versatilists) showed non-uniform distributions throughout the year (Rayleigh test, p < 0.05). Generalists and versatilists were abundant in April and February, respectively (pre-monsoon), whereas specialists were more abundant from October to November (post-monsoon) (Fig. 4b–d).

Influence of microenvironment on butterfly assemblages

Environmental abiotic parameters (Temp, RH, LI, and WS) and vegetation variables (CC, TD, ShD, and HD) were analysed in this study to understand their impact on butterfly assemblage (Table 4). OF showed the highest mean Arial temperature (°C) (30.51 ± 4.35) followed by RF (29.89 ± 3.85) and DF (29.38 ± 4.49). RH (%) was recorded highest in DF (60.40 ± 4.52) followed by RF (58.78 ± 4.01) and OF (57.80 ± 4.30). LI (×100 lux) was recorded highest in OF (450.80 ± 64.53) followed by RF (356.65 ± 61.32) and DF (250.05 ± 46.30). WS (m/s) was recorded highest in OF (0.94 ± 0.16) followed by RF (0.66 ± 0.12) and DF (0.50 ± 0.14). CC (%) was recorded highest DF (42.30 ± 5.76) followed by RF (28.31 ± 10.42) and OF (21.18 ± 9.05). TD

Fig. 2 Illustration of sample-based interpolation (rarefaction) of butterfly species, with extrapolation depicted by the dotted line
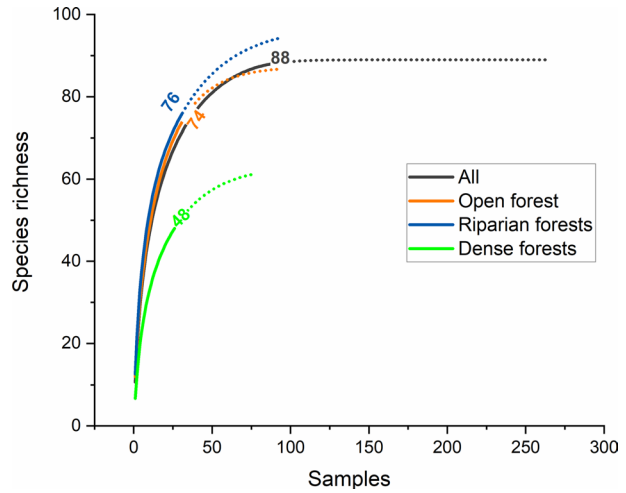
Table 2 Additive species diversity of butterflies at nested spatial scales in the study carried out at Koraput of southern Odisha, Eastern Ghats of India

	Level	Species richness (S)				p	Shannon–Wiener index (H')				p
		Obs	Exp	Obs.%	Exp.%		Obs	Exp	Obs.%	Exp.%	
All species	$\alpha_{transect}$	15.4	26.09	17.5	29.64	ns	8.03	17.09	62.44	82.28	ns
	$\beta_{transect}$	28.18	30.35	32.02	34.48	ns	2.22	1.55	17.26	7.46	*
	$\beta_{forest\ type}$	21.57	17.76	24.51	20.18	*	1.37	1.09	10.65	5.24	*
	$\beta_{elevation}$	22.85	13.8	25.97	15.68	*	1.24	1.04	9.65	5.00	*
	γ	88					12.86				
Generalist	$\alpha_{transect}$	5.38	8.22	23.39	35.73	ns	3.31	5.8	43.44	62.43	ns
	$\beta_{transect}$	7.82	6.56	34	28.52	*	1.97	1.39	25.85	14.96	*
	$\beta_{forest\ type}$	5.57	4.21	24.22	18.30	*	1.23	1.07	16.14	11.51	*
	$\beta_{elevation}$	4.23	4.01	18.39	17.43	ns	1.11	1.03	14.57	11.08	*
	γ	23					7.62				
Versatilist	$\alpha_{transect}$	9.84	17.51	19.68	35.02	ns	5.1	10.82	51.89	74.82	ns
	$\beta_{transect}$	17.09	17.91	34.18	35.82	ns	2.1	1.51	21.36	10.44	*
	$\beta_{forest\ type}$	14.45	9.32	28.9	18.64	*	1.41	1.09	14.34	7.53	*
	$\beta_{elevation}$	8.62	5.26	17.24	10.52	*	1.22	1.04	12.41	7.192	*
	γ	50					9.83				
Specialist	$\alpha_{transect}$	2.07	4.65	13.8	30.98	ns	1.49	3.25	21.05	42.81	ns
	$\beta_{transect}$	3.85	6	25.67	39.97	ns	2.41	1.98	34.04	26.08	*
	$\beta_{forest\ type}$	2.79	1.74	18.6	11.59	*	1.38	1.17	19.49	15.41	*
	$\beta_{elevation}$	6.29	2.62	41.93	17.45	*	1.8	1.19	25.42	15.67	*
	γ	15					7.08				

Observed (Obs.) versus Expected (Exp.) values and their percentages (%) for Species richness (S) and Shannon–Wiener index (H'), at different spatial scales

*Significant values of $p < 0.05$ level, means that the observed value of alpha or beta diversity is significantly larger or smaller than the null estimate produced after 1000 randomizations; ns- not significant

(trees/ha) was highest in DF (1189.20 ± 131.14) followed by OF (662.08 ± 91.67) and RF (578.04 ± 81.48). ShD (shrubs/ha) was highest in OF (6423.84 ± 815.07) followed by DF (5654.61 ± 601.12) and RF (4477.84 ± 443.19). HD (herbs/m2) was highest in OF (39.14 ± 4.17) followed by DF (25.82 ± 2.57) and RF (24.25 ± 3.30) (Table 4). The multiple linear regression model indicated that RH is the most important predictor of generalists ($R^2 = 0.231$, p = 0.001), while RH, ShD, and Temp all predict overall species richness ($R^2 = 0.402$, p = 0.001). Furthermore, abundance of generalist species is predicted by RH ($R^2 = 0.222$, p = 0.001), while RH and ShD predict overall butterfly abundance ($R^2 = 0.263$, p = 0.001). RH and ShD have negative effects on butterfly assemblages whereas temperature has positive effect (Table 5). However, there are no significant predictors of richness and abundance in the versatilist and specialist groups. Furthermore, the effects of predictors on species assemblages varied according to forest type. ShD is a major predictor of butterfly abundance in OF ($R^2 = 0.237$, p = 0.02), whereas Temp in RF ($R^2 = 0.381$, p = 0.002). RH was an important predictor of species richness in RF ($R^2 = 0.459$, p = 0.001) and DF ($R^2 = 0.399$, p = 0.004). Furthermore, in DF, HD had a positive effect on butterfly abundance, whereas canopy cover and RH had a negative effect ($R^2 = 0.649$, p = 0.001) (Table 5).

Discussion

This study investigated how microenvironments influence the functional composition and phenology of tropical dry forest butterflies in the Eastern Ghats of India. Environmental effects on butterflies mostly contribute to the shaping of community structure, and knowledge of their distribution is crucial for understanding the dynamics of biological communities (Walla et al. 2004; Soga and Koike 2013). In this study, the majority of generalist species including, the most abundant Nymphalidae family, are typical of vagrant species and were recorded from disturbed sites in the early stages of succession similar to the findings of Brito et al. (2014). This is also supported by a previous study by Mahata et al. (2023) in this region which reported that the tolerant species are mainly found in open forests which are prone to disturbances. It was reported that specialist species are generally prone to extinction in fragmented landscapes (Soga and Koike 2013). Our study showed that open
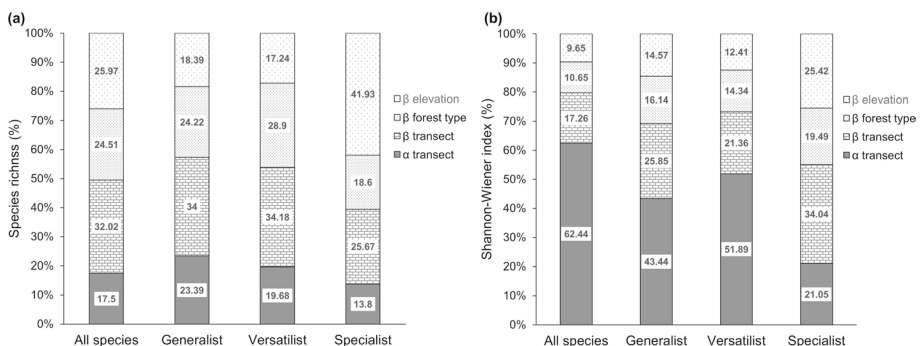

Fig. 3 Additive partitioning of gamma diversity (γ) for butterflies, illustrating the contribution (%) of alpha (α) and beta (β) components. Diversity is measured using **a** species richness (S) and **b** the Shannon–Wiener index (H′)

Table 3 Phenology of butterflies based on habitat and functional groups in the study at Koraput of southern Odisha, Eastern Ghats of India

	Sample size (N)	Mean vector (μ)	Mean date	Angular deviation (s)	Rayleigh test (z)	p
Habitat type						
Open forest	1362	99.471	11-04-2017	141.919	5.899	0.050
Riparian forest	1449	67.921	10-03-2017	90.771	240.257	<0.001
Dense forest	532	87.742	24-03-2017	84.438	124.603	<0.001
Functional group						
Generalist	1119	95.376	07-04-2017	75.735	406.812	<0.001
Versatilist	2124	42.039	12-02-2017	117.486	63.629	<0.001
Specialist	100	301.680	02-11-2016	100.660	9.191	0.010

Watson-Williams F Test for forest type: F=15.9201 (p<0.001) and for functional group F=134.9396 (p<0.001)
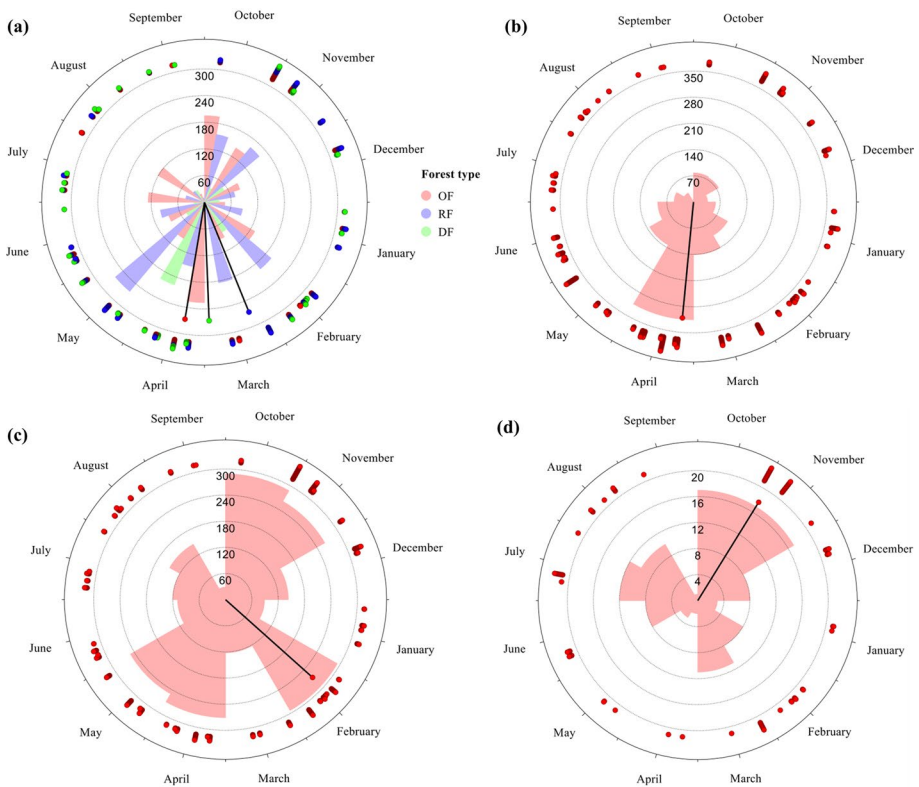
Fig. 4 Monthly abundances recorded for butterflies across different functional traits: **a** Total assemblages, **b** Generalists, **c** Versatilists, and **d** Specialists

Table 4 Environmental parameters (mean ±SD) of different forest types at different elevation gradients in Koraput of southern Odisha, Eastern Ghats of India

Elevation (m)	Forest types	Temp (°C)	RH (%)	LI (x lux)	WS (m/s)	CC (%)	TD (Trees/ha)	ShD (Shrubs/ha)	HD (Herbs/m²)
400–650	OF	30.51±4.35	57.80±10.16	450.80±102.69	0.94±0.16	21.18±5.05	443.08±159.14	2944.47±652.06	39.71±5.73
	RF	31.43±4.11	63.54±7.89	378.49±123.45	0.12±0.04	27.05±2.38	603.51±155.33	4783.49±1732.04	23.74±11.16
	DF	29.11±3.10	61.95±6.99	199.21±64.97	0.19±0.06	45.34±4.78	753.75±249.55	3138.05±1171.67	31.29±12.39
650–900	OF	33.35±4.42	45±14.24	616.23±193.54	1.94±0.20	16.39±4.06	460.911±186.47	7330.61±2394.29	34.12±6.69
	RF	29.58±3.07	56.75±6.01	408.32±104.92	0.76±0.40	33.94±6.25	431.62±117.13	2465.61±315.84	9.71±2.61
	DF	32.36±4.8	55.14±11.46	304.66±114.93	0.81±0.24	40.31±9.63	905.27±244.46	5797.24±1562.40	15.53±8.93
900–1150	OF	27.96±5.81	62.54±12.14	324.04±139.99	0.51±0.17	19.17±2.34	354.72±133	7208.35±489.04	27.92±7.09
	RF	31.03±4.67	54.06±12.06	554.76±159.23	1.24±0.50	22.34±11.63	409.98±236.82	5068.77±937.34	39.84±5.61
	DF	31.18±5.65	51.27±13.41	395.24±131.18	0.69±0.19	41.18±3.17	1022.10±63.91	7840.04±1706.57	31.43±5.82
1150–1400	OF	30.06±3.23	52.91±15.15	600.19±124.14	1.08±0.25	16.47±4.49	495.28±168.06	9592.46±1467.14	54.59±11.89
	RF	27.44±3.02	59.65±7.47	228.17±87.58	0.64±0.23	29.86±6.31	697.73±262.28	5348.95±1531.89	23.84±6.81
	DF	25.42±2.19	70.25±7.79	158.05±82.85	0.61±0.26	43.76±3.45	1088.61±162.97	8150.79±2435.04	25.71±8.11

Temp temperature, *RH* relative humidity, *LI* light intensity, *WS* wind speed, *CC* canopy cover, *TD* tree density, *ShD* shrub density, *HD* herb density, *OF* open forest, *RF* riparian forest, *DF* dense forest

forests, which have been under threat in recent times (Reddy et al. 2013; Dash et al. 2017), contributed more than 50% of specialist species, indicating that conservation is important for the long-term survival of habitat specialists in highly fragmented landscapes. In addition, butterflies prefer open forests which provide essential biotic resources (larval host plants, nectar plants) and abiotic conditions required by forest-inhabiting butterflies (Viljur et al. 2020; Mahata et al. 2023). Furthermore, conserving large and well-connected fragments has been recommended by Soga and Koike (2013).

The beta diversity analysis of butterfly species richness across various transects yielded no statistically significant deviations from the expected values. This implies that all butterfly communities are essentially sub-samples of the same overarching species pool. The variations in the Shannon–Wiener index indicate differences in dominance patterns among communities across various transects (Ribeiro et al. 2008). The Shannon–Wiener index places more weight on common species than species richness, indicating that the beta diversity among transects suggests differences in populations of some of the most abundant species. This is also suggested by significantly higher beta diversity among transects for generalist species in this study (Ribeiro et al. 2008). Both diversity indices showed higher beta diversity among each forest type within each study site than expected by chance. This means that butterflies are not randomly distributed inside forests of the study sites, which can be explained by intra-specific aggregation on higher hierarchical levels, i.e., $\beta_{\text{forest type}}$ and $\beta_{\text{elevation}}$ (Ribeiro et al. 2008). This is also supported by the non-homogenous distribution of larval and adult food resources in forest types of the study sites (Hamer et al. 2006).

Table 5 Multiple Linear Regression demonstrated the impact of the microenvironment on butterfly assemblages in the study at Koraput of southern Odisha, Eastern Ghats of India

Components	Regression coefficient (R^2)	ANOVA (Significance value)	Predictors	Standardised β coefficients	Collinearity (Tolerance)
Open forest					
Abundance	0.237	0.022	Shrub density	− 0.487	1
Riparian forest					
Richness	0.459	0.001	Relative humidity	− 0.678	1
Abundance	0.381	0.002	Temperature	0.617	1
Dense forest					
Richness	0.399	0.004	Relative humidity	− 0.631	1
Abundance	0.649	0.001	Canopy cover	− 0.599	0.787
			Relative humidity	− 0.459	0.883
			Herb density	0.444	0.838
Total assemblages					
Richness	0.402	0.001	Relative humidity	− 0.353	0.576
			Shrub density	− 0.286	1
			Temperature	0.273	0.576
Abundance	0.263	0.001	Relative humidity	− 0.417	1
			Shrub density	− 0.303	1
Generalist					
Richness	0.231	0.001	Relative humidity	− 0.48	1
Abundance	0.222	0.001	Relative humidity	− 0.472	1

Versatilist and Specialist groups have no significant predictors for both richness and abundance

Apart from food supplies, vegetation structure is also connected with microhabitat factors such as temperature, humidity, and luminance, as well as anthropogenic disturbance, which alters the species assemblages in the forest types for the investigated area (Ribeiro et al. 2008; Mahata et al. 2023). When comparing the different forest types, butterflies tend to favour riparian forests due to the favourable microclimate as well as the availability of suitable food and water resources in these habitats (Mahata et al. 2023). This is also supported by the present study, where the rarefaction/extrapolation curve indicated additional survey locations are likely to yield new species in riparian forests (Fig. 2). On the contrary, the rarefaction/extrapolation curve tends to approach a horizontal asymptote following an initial rise in open and dense forests. This pattern suggests that the count of observed species remains constant after the initial period, attributable to homogeneous vegetation, a dense canopy in dense forests, and the relatively elevated temperature and low humidity associated with disturbances in open forest areas (Mahata et al. 2023). The contribution of β diversity among transects ($\beta_{transect}$) to total gamma diversity was notably larger than that of the highest hierarchical level ($\beta_{elevation}$), except for the specialist group. This suggests that landscape attributes were more favourable for the specialist group than the forest type. Greater β diversity was observed at the elevation zone scale compared to habitat or finer scales in this study, supported by the findings of Zografou et al. (2017). Similar results were also found from studies carried out in this region (Mahata et al. 2019a, 2023; Mahata and Palita 2023), which reported that the species richness in the eastern high-elevation ranges (Koraput Plateau), is higher than that of the western low elevation zone (Jeypore Plateau). Furthermore, habitat specialist species were predominantly concentrated at higher elevations and were almost missing from lowland regions, exhibiting a clear preference for cold areas at mid- or high elevations and habitat availability, i.e., percentage of grasslands (Stefanescu et al. 2011; Mahata et al. 2023). This finding underscores the significance of considering elevation zones in conservation planning for specialist species.

Various studies show that peaks of tropical butterfly abundance and diversity are biannual and occur during pre-wet and post-wet seasons (Grøtan et al. 2014; Con and Lien 2015; Gupta et al. 2019) although the annual peak of diversity recorded in post-wet seasons by Kunte (1997) in Western Ghats and pre-wet seasons by Bhardwaj et al. (2012) in the Tons valley, Western Himalayas of India. Our results also support the annual peak abundance in pre-wet seasons due to stronger effects of temperature than relative humidity, a finding similar to that of Grøtan et al. (2014). Similarly, the peak abundance of butterflies in pre-wet seasons has also been recorded previously from this region (Mahata and Palita 2023). One of the most important findings of the present study was the distribution of the functional groups throughout the year, mainly concentrated during the most favourable seasons, usually spring and summer (Wynter-Blyth 1957; Kunte 2000; Pozo et al. 2008). The abundance and diversity of generalist and versatilist species peaked during the pre-wet seasons as abundant family Nymphalidae, Lycaenidae, and Pieridae increased their number at the onset of monsoon due to the availability of mud-puddling sites and nectar sources in riparian forest areas (Kunte 2000). Specialist species were concentrated during the second most favourable post-monsoon period (Wynter-Blyth 1957) as these climatic conditions of monsoon support greater numbers of plant species (Harrison et al. 2020) and provide suitable phenophase for growth of the caterpillars (Kunte 1997).

Local landscape factors play a crucial role in the functional species composition and phenology of butterflies (Rosin et al. 2012; Brito et al. 2014). Local increases in temperature, humidity, and the duration of the growing season may imply potential links between the observed phenological alterations and climate change. Vegetation structure (mainly canopy openness) and climate (temperature) are known to be significant predictors of

butterfly communities at the habitat level (Barlow et al. 2007; Dolia et al. 2008). In this study, varying microclimatic factors (Temp, RH, LI, WS) and vegetation components (CC, TD, ShD, HD) in both forest types and landscapes formed a mosaic ecosystem for butterfly functional groups. Similar forest landscape heterogeneity is crucial for maintaining butterfly diversity at the landscape scale (Viljur et al. 2020; Mahata et al. 2023). Zografou et al. (2021) studied 18 butterfly species, of which 13 species showed shifts in mean flight date and duration due to varying larval trophic specialization, larval diet makeup, and voltinism affected by seasonal temperature. Furthermore, Stefanescu et al. (2011) studied Mediterranean butterflies and reported that the number of generalists dropped during severe land use changes associated with aridity and specialists were negatively impacted by temperature. Habitat structure can affect the abundance and distribution of host plants (Stanton 1982), nectar plants (Murphy 1983), predators (Montllor and Bernays 1993), and ants tending larvae (Pierce and Elgar 1985). In this study, the temperature-humidity coupling effect along with shrub density provided 40.2% information for species richness whereas 26.3% for abundance (Table 5) supported by various studies (Pollard 1988; Bhardwaj et al. 2012; Gupta et al. 2019). Studies on the impacts of climate change on butterfly phenology in the northwest Mediterranean Basin by Stefanescu et al. (2003) revealed that higher temperatures tend to result in earlier phenological while precipitation has the opposite effect in specific months. Similar results were found in the study of Lesica and Kittelson (2010). Furthermore, studies on British butterflies (Roy and Sparks 2000) observed climate warming on the order of 1 °C might move forward the initial and peak appearance of most butterflies by 2–10 days owing to interactions with other species and changes in land use. In this study, relative humidity is predominant over temperature for species richness (Table 5) and became a major predictor for assemblages of generalist species (Gupta et al. 2019). However, no specific predictors have been recorded for versatilists and specialists in this study; hypothesized larval host plant diversity are better predictors for these groups (Menéndez et al. 2007; Brückmann et al. 2010). Reduced butterfly detectability was due to the growing understory canopy in this study, which was managed beating shrub branches during peak butterfly season (Ohwaki et al. 2017).

Conclusion

Our comprehensive investigation of the biodiverse Eastern Ghats of India has provided a deep understanding of the intricate dynamics governing butterfly populations within tropical dry forests. Despite the ongoing anthropogenic transformations, these forests stand out as crucial reservoirs for species conservation, offering unique insights into the functional roles played by ecological traits. The beta diversity analysis uncovered disparities in common species populations, a reflection of the uneven distribution of resources within the study site forests. Notably, landscape attributes demonstrated a preference for specialists, underscoring the pronounced influence of environmental factors on butterfly populations. Elevational gradients emerged as pivotal factors shaping habitat specialization, emphasizing the necessity of incorporating spatial considerations into conservation planning. The elucidation of temporal patterns in butterfly abundance and diversity revealed distinct preferences among generalists, versatilists, and specialists. Seasonal variations were evident, with versatilists and generalists favouring pre-wet seasons, while specialists exhibited a preference for post-wet seasons, aligning with the suitability of microenvironmental

factors during these periods. In essence, our research underscores the critical importance of understanding spatial and temporal distribution patterns, especially within the context of the tropical dry deciduous forests of India. The insights gained from this study serve as a foundation for future research endeavours and contribute valuable knowledge for the effective conservation and management of butterfly populations in this ecologically significant region.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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