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Ecological monitoring and indicator taxa: butterfly communities in heterogeneous landscapes of the Western Ghats and Malabar coast, India

Deepak Naik[1] · R. Shyama Prasad Rao[2] · Krushnamegh Kunte[3] · Mohammed S. Mustak[1]

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Abstract
As the pace of socioeconomic developments continues to accelerate, the environmental degradation and biodiversity loss become the norm. While it is crucial to constantly monitor and assess ecological impacts, baseline data are scanty for ecologically sensitive regions and biodiversity hotspots such as the Western Ghats. With their great public appeal and ease to work with, butterflies are excellent communities to monitor the ecological health. To characterize the baseline patterns of butterfly communities, using time-constrained counts, we surveyed eight heterogeneous landscapes of the coastal plains of the Western Ghats. We recorded 43,118 individuals and 175 species, with large differences in their diversity and species-specific abundances among habitats. The coastal and semi-evergreen-forest habitats were at the two extremes with intermediate patterns in agricultural and other habitats that suffered diverse anthropogenic pressures. Using indicator value analysis, 22 habitat-specific and several shared indicator species were identified. Even some of the most abundant species showed distinct niches, and therefore can be used as indicator species to monitor community dynamics. Patterns of numerous habitat-specific host-plant butterfly species pairs that were identified were discussed in relation to butterfly abundance and conservation.
Implications for insect conservation This study has implications for insect conservation by providing important baseline data on butterfly taxa for future monitoring and assessment of this ecologically sensitive region.

Keywords Biodiversity · Eco-informatics · Ecological health monitoring · Habitat degradation and loss · Indicator taxa

Introduction

Continued human wellbeing depends on sustained socioeconomic/industrial developments, which in turn depend on the products and services from the natural ecosystems. However, fast pace of such developments severely affects the natural ecosystems—leading to environmental degradation and habitat/biodiversity loss—with little scope for their recovery. It is therefore imperative that we constantly monitor ecological health (interchangeable with ecosystem health to mean "well-functioning") using varied indicators (Costanza 2012; De Cáceres et al. 2010; Karr 1996; Siddig et al. 2016). However, even baseline data are scarce and therefore there is an urgent need to understand the ecological patterns and their dynamics/drivers at various levels.

Apart from serving numerous ecological functions and playing a role in maintaining a healthy ecosystem, butterflies as a taxon has a great public appeal. Butterflies can serve as good ecological indicators (species/taxa that can be associated with a community or habitat type) as they quickly respond to the changes in the environment such as community dynamics and/or vegetation patterns that influence their species composition (Carignan and Villard 2002; De Cáceres et al. 2010; Erhardt and Thomas 1991; Rákosy and Schmitt 2011). Butterflies are easy to monitor, and regular monitoring of their population can provide an early warning of the changes in the environment (Sreekumar and Balakrishnan 2001). They are considered as the umbrella species in nature conservation (New 1997), and studies on

✉ Mohammed S. Mustak
msmustak@gmail.com

1 Department of Applied Zoology, Mangalore University, Mangalagangothri 574199, India

2 Biostatistics and Bioinformatics Division, Yenepoya Research Center, Yenepoya University, Mangalore 575018, India

3 National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bengaluru 560065, India

the population/community ecology of even common species were known to provide valuable information on the status of other species/taxa (Pearman and Weber 2007; Pollard 1991). Understanding the community structure of butterflies at local level is therefore useful to track the rapid changes happening in the landscape due to anthropogenic activity (Purvis and Hector 2000).

One such anthropogenically active but ecologically sensitive region is the Western Ghats (a mountain ecosystem) in the Indian peninsula—a major biodiversity hotspot (Gadgil 1996). Apart from driving the macroclimatic and rainfall patterns of India, it provides numerous ecological products and services. Although deeply linked to cultural roots of the people; the Western Ghats, especially in the coastal regions, is fast undergoing socioeconomic, agricultural, and industrial developments (Jha et al. 2000). As a result, it is facing rapid environmental degradation (Jha et al. 2000; Jitendra 2019; Mittermeier et al. 1998; Rao and Girish 2007). With limited ecological assessment (Gaonkar 1996) and virtually no monitoring programs, even the baseline information on the ecological health of this region is scanty. Further, although this region is an ecological hotspot, little is known about the local community structure and distribution pattern of various taxa, including butterflies (Faith 1992). Such studies will help both ecological monitoring and prioritize the conservation needs of the region (Gadgil 1996).

Given their ease and entice, butterflies were often studied as a key taxon in the context of conservation and assessment in other mountain ecosystems which are undergoing transformations due to various anthropogenic pressures such as climate change, tourism, and agricultural activity. For example, butterfly assemblages of Eastern Himalaya, a mountain ecosystem, were explored along the elevation gradient (Acharya and Vijayan 2015; Dewan et al. 2019), along trekking corridor with human disturbance gradient (Chettri 2015), or agriculture-forest land use gradient (Sharma et al. 2020). Similarly, global warming and anthropogenic land use have been shown to affect butterfly species and range shifts in Neotropical mountains (Molina-Martínez et al. 2016). Thus, human-modified ecosystems both inside and outside the protected areas (Chettri 2015; Sharma et al. 2020), as well as in agriculture (Munyuli 2013) and urban landscapes (Paul and Sulthana 2020) are key repositories of butterflies for conservation (Bonebrake et al. 2010).

There are some studies on the patterns of butterfly diversity and species distribution in different regions of Western Ghats (Kunte et al. 1999; Nayak et al. 2004), including northern (Kunte 1997; 2001; Padhye et al. 2006), and Anaikatty hills (Eswaran and Pramod 2005), and Kudremuk National Park in the mid Western Ghats (Mohandas 2004; Mohandas and Remadevi 2019). However, there is a need to understand the fine-scale patterns of the distribution and composition of butterflies of the Western Ghats (Padhye et al. 2012). Further, there are no studies on the diversity and composition of butterfly communities of the coastal regions of Western Ghats (Naik and Mustak 2016).

Thus, the aim of this paper was to study the butterfly community structure in the unexplored coastal plains and foothills of the Western Ghats, and thus provide a baseline information of this indicator taxon for the future monitoring of the anthropogenically fast-changing but ecologically sensitive coastal Western Ghats. Further, we also wanted to explore how species were associated with different habitat types. We surveyed eight heterogeneous landscapes in the coastal plains and foothills of Western Ghats in the Dakshina Kannada district. Using a large sample size of 43,118 individuals in 175 species, we present the patterns of occurrence/diversity and abundance of butterfly taxon. Our work provides an important dataset for the future assessment/conservation of butterflies of this ecoregion.

Materials and methods

Study sites

The present study was carried out in eight heterogeneous sites/landscapes in the coastal plains and foot hills of the Western Ghats situated in Dakshina Kannada district of Karnataka, India. The region has a tropical climate and receives around 3900 mm of rainfall annually (India Meteorological Department [IMD], https://mausam.imd.gov.in/). The sites were chosen based on distinct landscape elements namely Agriculture (AR), Botanical arboretum (BA), Coastal (CO), Laterite mixed shrubby (LMS), Modified forest (MF), Mixed moist deciduous (MMD), Rocky crop (RC), and Semi evergreen (SE). The last three study sites (Mixed moist deciduous, Rocky crop, and Semi evergreen) were located inside the protected areas. Elevation of sites ranged from 4 to 304 m. There was no physical demarcation of study sites/habitats from their surroundings, but their overall size ranged from approximately 1.6 sq km (Coastal) and 1.9 sq km (Botanical arboretum) to several hundreds of sq km (Semi evergreen). Location map (Fig. S1) and detailed descriptions of the sites are given in the Supplemental Information. Relevant permission (No. PCCF/C/GL-01/2016-17) for the field survey was obtained from the Principal Chief Conservator of Forests, Karnataka Forest Department, Bengaluru. No butterflies were killed or collected in this study.

Butterfly survey

Six consecutive 500-m transect lines (3 km in total) were set up (with peg markings at every 100 m) in each of the eight landscapes. There were no major transitions/ecotones within a site. The placement of the transect trails (which were not rectilinear) was chosen to obtain the best representation of the habitat micro-heterogeneity/diversity. The study was conducted for two consecutive years from November 2016 to October 2018. Each study site/landscape was visited twice a month in the interval of 15 days, and sampling was carried out (irrespective of weather conditions) during the peak activity of butterflies—between the time from 09:30 AM to 1:00 PM. Each transect was covered in 30 min (for example: first 0.5 km—9:30 AM to 10:00 AM, second 0.5 km—10:00 AM to 10:30 AM, and so on, a total of 3 h for 3 km) (Suman et al. 2021). Butterfly quantitative data were collected using the time-constrained count method by walking in a slow but steady pace and counting the individuals present within a width of 5 m on either side of the transect (Kadlec et al. 2012; Pollard 1977; Suman et al. 2021). Individual butterflies were identified on the move by a surveyor and noted (by a field assistant) to the species level (Gunathilagaraj et al. 1998; Kehimkar 2008; Kunte 2000). However, given the difficulty of identification in the field, some individuals where identified only to the genus level (Table S1).

Common plants present along the transect in each habitat were identified to the species level (a few were identified only to the genus level). It was not a systematic or quantitative survey of plants, but just an indicative presence-absence data (Table S2). The species that were known to be potential host plants for the butterflies of the Western Ghats were noted based on literature (Kunte et al. 2021; Nitin et al. 2018).

Data/statistical analyses

The six transects were essentially six spatial replicates for each habitat (Table S1). Together, there were 288 samples (6 replicates × 48 days of census) for each site. Forty eight census data were pooled. Replicates were analyzed separately (Table S3), or where appropriate (given low number of individuals for many species) they were combined; and abundance and species richness were enumerated for each site (Table 1). Relative abundances were calculated using $\frac{x_i}{N}$, and where appropriate normalized abundances were calculated using $\frac{x_i - \min(x)}{\max(x) - \min(x)}$ (where x is the absolute frequency and N is the total), so that they are comparable across sites and/or species. Percentage of species and individuals belonging to each taxonomic family were represented as a pie chart using Excel. Rank abundance graph was plotted in Excel using the ranked (descending) relative proportions of species (Fig. 1A and B). Since the sample sizes were unequal among sites, rarefied species richness was estimated using rarefaction (https://strata.uga.edu/software/win/aRarefactWin.exe; Holland 2003) and rarefaction curves were plotted (along with 95% confidence interval) for each habitat to compare the relation between the number of species versus the total number of individuals. Although sampling effort was equal among sites, rarefaction is a special case wherein species richness is compared based on equal number of individuals (but not equal sampling effort). Finally, diversity accumulation curves were computed using iNEXT Online tool (https://chao.shinyapps.io/iNEXTOnline/). The iNEXT estimates species diversity as Hill numbers (effective number of species) using rarefaction and extrapolation (Chao et al. 2014).

Various diversity indices were calculated as mentioned previously (Kunte et al. 1999; Rao and Girish 2007). Briefly, α-diversity for a site was calculated as Shannon's $H' = -\sum p_i \times ln(p_i)$, and Simpson's $1 - D = \sum \left(\frac{n}{N}\right)^2$, where p_i is the proportion of ith species, n is the frequency of nth species, and N is the total frequency within a site

Table 1 Diversity attributes of butterfly communities in heterogeneous landscapes of coastal plains of Western Ghats

Site	N[a]	# of species[a,b]	Rarefied richness[c]	Alpha diversity		Evenness	Dominance	# of unique species[d]
				Shannon's	Simpson's			
AR	5500	95 (90.4, 99.6)	88.8 (84.6, 92.9)	3.429	0.953	0.753	0.047	2
BA	7345	114 (110.7, 117.4)	106.2 (101.7, 110.7)	3.614	0.951	0.763	0.049	1
CO	3622	65 (61.4, 68.6)	64.7 (63.6, 65.8)	3.020	0.919	0.723	0.081	3
LMS	4894	109 (103.4, 114.6)	102.9 (98.7, 107.1)	3.529	0.948	0.752	0.052	4
MF	6032	120 (114.4, 125.6)	111.5 (106.8, 116.2)	3.769	0.964	0.787	0.036	1
MMD	3802	112 (104.4, 119.6)	110.1 (107.6, 112.7)	3.717	0.960	0.788	0.040	5
RC	3504	112 (106.4, 117.6)	112	3.635	0.954	0.770	0.046	3
SE	8419	128 (122.9, 133.1)	113.3 (107.7, 119)	3.737	0.963	0.770	0.037	13
Total	43,118	175 (168.4, 181.6)	133.5 (126.6, 140.5)	4.049	0.973	0.784	0.027	32

[a]See Table S3 for statistics on individual (N) and species richness based on spatial replication data

[b]Values in parenthesis are 95% confidence intervals, based on iNEXT estimator (Chao et al. 2014). See Fig. S2A

[c]With reference to RC site, and values in parenthesis are 95% confidence intervals. See Fig. 1C

[d]See Table S1 for further details, and Table S4 for additional diversity attributes

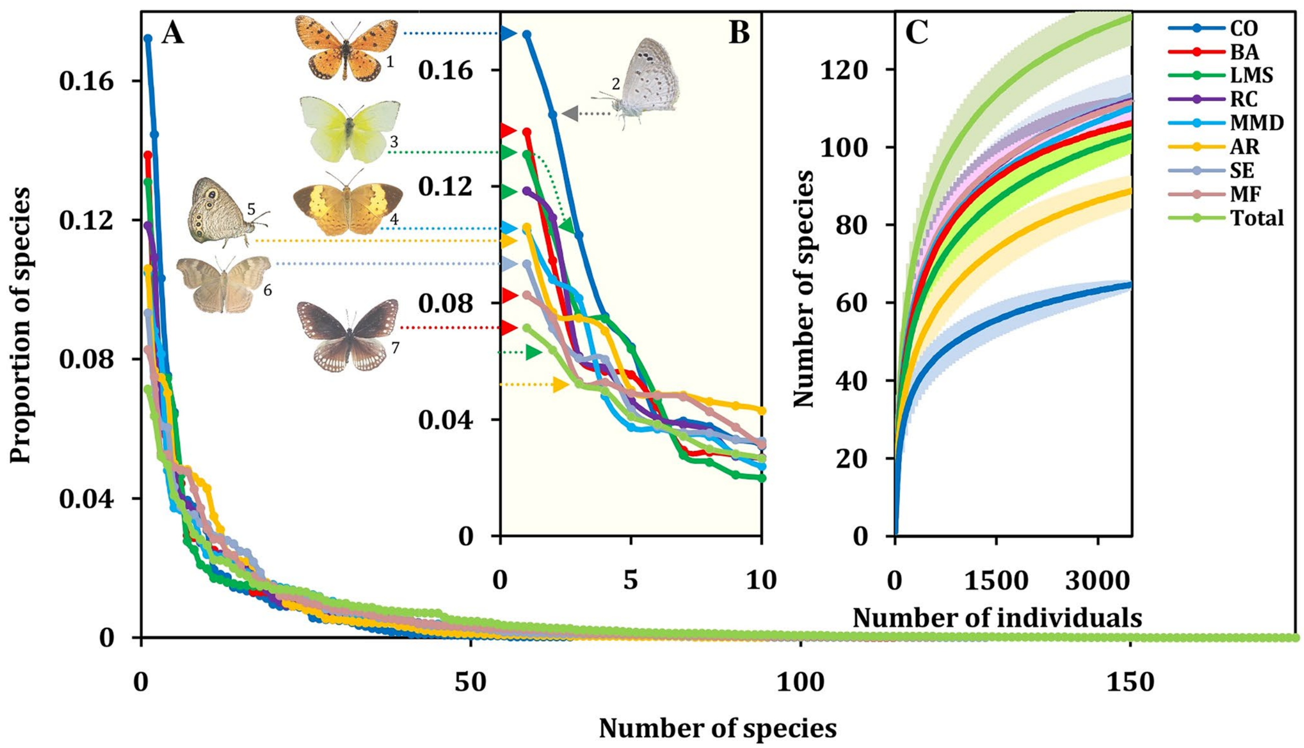

Fig. 1 Patterns of butterfly communities in heterogeneous landscapes. **A**, **B** Rank abundance [**A** full and **B** expanded view], and **C** rarefaction curves (with 95% confidence interval) of butterflies in different habitats. The habitat abbreviations are: agriculture (AR), botanical arboretum (BA), coastal (CO), laterite mixed shrubby (LMS), modified forest (MF), mixed moist deciduous (MMD), rocky crop (RC), and semi evergreen (SE). flagged species in the figure are (1) *Acraea terpsicore*, (2) *Zizina otis*, (3) *Catopsilia* spp. (green arrows), (4) *Cupha erymanthis*, (5) *Ypthima huebneri* (orange arrows), (6) *Junonia iphita*, and (7) *Euploea* spp. (red arrows). See Fig. S2 for diversity accumulation curves. (Color figure online)

(Magurran 1988). Proportion of unshared species across sites (β-diversity) was calculated as Whittaker's $\beta_W = \frac{\gamma}{\alpha} - 1$, where α (α-diversity) is the mean number of species between sites and γ (γ-diversity) is the total number of species between them (Whittaker 1960). Species evenness within a site was calculated as Pielou's $J' = H'/H'_{max}$, where $H'_{max} = \ln(S)$ and S is the number of species. Further, habitat equitability or evenness of species across sites was calculated as Simpson's $E = D/D_{max}$, where $D = \frac{1}{\sum p_i^2}$ and D_{max} is the number of habitats (Magurran 1988), and plotted against normalized abundance. Extent of species dominance within a site was calculated as $D = 1 -$ Simpson's index of diversity. Numerous other relevant indices were also computed (see Supplemental Information and Table S4). Diversity indices were calculated using PAST (version 3.26) software (Hammer et al. 2001).

Hierarchical Cluster Analysis (HCA) and Non-metric Multidimensional Scaling (NMDS) were performed to visualize the relationship or similarities among study sites based on species assemblage, or butterfly species based on habitat preferences. HCA was based on Bray–Curtis dissimilarity (a measure of β diversity) as a distance and was done in PAST software using UPGMA as the clustering algorithm. NMDS was performed using metaMDS() in vegan package in R software (https://rdrr.io/cran/vegan/man/metaMDS.html). Visualization was done by plotting the NMDS scores in Excel. NMDS is a rank-based/non-parametric approach and better (than PCA, for example) when the data matrix contains a lot of zero values (Legendre and Gallagher 2001). The Bray–Curtis dissimilarity (a measure of β-diversity)—a semimetric/abundance-based index was used as the distance and it was computed on relative abundances (Greenacre and Primicerio 2013; Schroeder and Jenkins 2018). The number of reduced dimensions in NMDS was k = 3 such that NDMS stress was kept well below 0.15. In addition, heat map was done using heatpmap.2() in gplots package in R software (https://cran.r-project.org/web/packages/gplots/index.html) to visualize the occurrence/abundance of butterflies across habitats, and was based on the actual site-specific normalized abundance data.

Finally, we looked at conservation values (Kunte 2008, 2016) and indicator values (De Cáceres et al. 2010; Sharma et al. 2020) of butterfly species in relation to habitats. The conservation values were based on scoring (between 1 and 10) in four parameters (namely global distribution, local distribution, habitat preference, and occurrence/abundance status) with total score ranging from 4 to 40 as listed in Kunte (2008). The indicator values (IndVal) were based on possible combinations of groups of sites (or samples/transects) and selecting the combination for which the species can be best used as an indicator (De Cáceres et al. 2010; Sharma et al. 2020). The indicator value estimation was done using multipatt() in R indicspecies package which also gives p-values based on permutation test (De Cáceres et al. 2010). A default number of 999 permutations was used.

All statistical analyses, where explicitly not mentioned, were performed in R version 3.6.2. Further, where appropriate, distribution-free non-parametric analyses/tests were preferred. For example, Spearman's rank correlation, which is less sensitive to outliers, was used for habitat equitability or conservation value against species abundance. The significance of correlation coefficient was testing using cor.test() [which is based on t-distribution or approximation] in R. A Kruskal–Wallis post hoc test was performed using pairwise.wilcox.test() [with p.adjust.method = "BH"] in R for testing the significance of observed differences in the individual and species richness among sites based on spatial replication data. The EcoTest.individual() [which is based on a test statistics Z] in R rareNMtests package was used for comparing rarefaction curves (Cayuela et al. 2015).

Results

Species diversity and abundance

A total of 43,118 individuals belonging to 175 species were counted in the present study (Table 1 and S1). This represents 52% of butterfly species recorded in the Western Ghats (Nitin et al. 2018). Based on site-wise pooled data, the Coastal habitat contained the lowest number of species (61.4 to 68.6, 95% confidence intervals), while Semi evergreen habitat had the highest number of individuals (N = 8419) and species (122.9 to 133.1). Agriculture habitat had intermediate levels of individuals (N = 5500) and species (90.4 to 99.6). Despite having a lowest number of individuals (N = 3504), Rocky crop habitat had high species diversity (106.4 to 117.6) compared to Coastal and Agriculture habitats, for example. These differences/trends are reflected in the spatial replication data (Table S3) and are significant ($p < 0.05$, Kruskal–Wallis post hoc test). From the various diversity indices that have been calculated (Table 1 and S4), it is clear that the Coastal and Semi evergreen habitats were mostly in the two extremes with respect to the values of these various measures. A total of 32 site-specific unique species were observed with Semi evergreen habitat containing highest (n = 13) unique species (Table 1 and S1; see Supplemental Information). An overall summary of the data—rank abundance and rarefaction curves of butterflies in different habitats—has been presented in Fig. 1. From rank abundance graph (Fig. 1B) it is clear that a couple of species (such as *Acraea terpsicore* and *Zizina otis*) were far more abundant than others in Coastal habitat; and some species (such as *Catopsilia* spp. and *Euploea* spp.) were quite common across habitats. Rarefaction showed that if an equal number of individuals were to be sampled, Coastal habitat followed by Agriculture habitat had clearly lower species richness (Fig. 1C), while other habitats were not very distinct as their 95% CI overlapped among themselves. This is further reflected in the diversity accumulation curves (Fig. S2) as a function of number of individuals or number of transects. Further, the effective number of species (Hill numbers) in terms of Shannon diversity (order $q = 1$) and Simpson diversity ($q = 2$) quickly reached plateau indicating a good sampling effort. One key point is that Simpson diversity for Agriculture habitat is much higher compared to Laterite mixed shrubby habitat, for example, indicating a higher diversity of dominant species (Chao et al. 2014).

Taxonomically, Nymphalidae was the most abundant family in terms of species (30.9%) and individuals (52%) (Fig. 2A and B). Hesperiidae, in spite of having high number of species (n = 39, 22.3%), had relatively low number of individuals (N = 2258, 5.2%). On the contrary, Pieridae with low number of species (n = 15, 8.6%) had high proportion of individuals (N = 7073, 16.4%). Average number of individuals per species is given family- and habitat-wise in Fig. 2C (overall, 43,118 individuals/175 species = 246 individuals per species). Species in Pieridae were abundant across habitats. A plot of the total proportion of individuals versus the total proportion of species across habitats and families showed consistent habitat-wise variability, but overall grouping based on families (Fig. 2D).

The *Euploea* spp. (mostly *E. core*) were the most abundant (7.1%), followed by *Catopsilia* spp. (mostly *C. pomona*), *Ypthima huebneri*, and *Eurema hecabe* (Figs. 1, 2E, and 4). The top 10 (5.7%) species represented 43.5% of the individuals and top 37 (21.1%) species represented 80.2% of the individuals.

Relationships among species and habitats

Even very abundant species showed inconsistent presence among habitats (Fig. 2E). For example, *Euploea* spp. and *Catopsilia* spp.—the most abundant species overall—were relatively rare in forest (Moist mixed deciduous and Semi evergreen) habitats wherein *Neopithecops zalmora* was an abundant species (Fig. 2E). *Acraea terpsicore*, although not a unique species, was very biased to open (Agriculture and Coastal) habitats (Fig. 1 and 2E). Some of these patterns were consistent with the presence of habitat-specific host plants (Tables S2 and S5). No two species showed identical

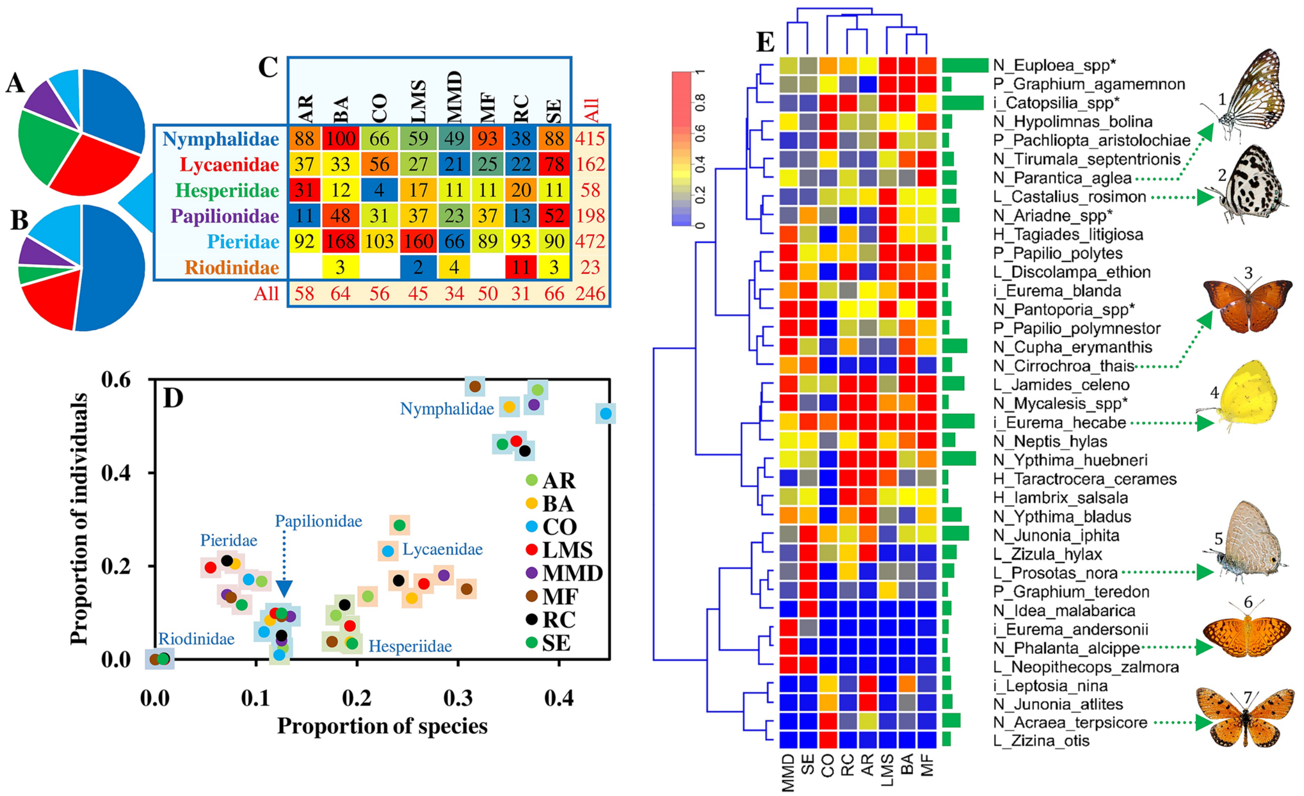

Fig. 2 Patterns of butterfly communities in heterogeneous landscapes. **A** Family-wise proportion of species and **B** individuals, **C** average number of individuals per species within family (rows) or habitat (columns), and **D** total proportion of individuals vs species in different butterfly families and study sites. Overall, nymphalids had high proportion of individuals, but pierids were the most abundant and hesperiids were the least. **E** Heat map shows the pattern of normalized abundance of 37 species (~21%) that make up ~80% of the total individuals (green bars next to heat map show total abundance). Most species were abundant only in a few habitats and therefore can be considered as indicator species such as (7) *Acraea terpsicore* in coastal and (3) *Cirrochroa thais* in forest habitats. *Eurema hecabe* was the most abundant species common to most habitats. The habitat abbreviations are: Agriculture (AR), Botanical arboretum (BA), Coastal (CO), Laterite mixed shrubby (LMS), Modified forest (MF), Mixed moist deciduous (MMD), Rocky crop (RC), and Semi evergreen (SE). Flagged species in the figure are (1) *Parantica aglea*, (2) *Castalius rosimon*, (3) *Cirrochroa thais*, (4) *Eurema hecabe*, (5) *Prosotas nora*, (6) *Phalanta alcippe*, and (7) *Acraea terpsicore*. A and B pie chart sectors' color match font color of family names in C. (Color figure online)

patterns among habitats (Fig. 2E; see Supplemental Information). It should be noted that these patterns are only suggestive, as monitoring butterfly abundance has limitations due to ecology and behaviour of target species under different habitat types (Pellet et al. 2012).

The Botanical arboretum, Laterite mixed shrubby, and Modified forest habitats were similar and formed a cluster along with Rocky crop and Agriculture (Fig. 3A). The Moist mixed deciduous and Semi evergreen habitats formed another group, while Coastal habitat was distinct. Figure 3B shows the numbers (upper triangular matrix) and proportions (lower triangular matrix) of shared species among sites and reflects the overall clustering seen in Fig. 3A. The NMDS (stress = 6.3E−5) of study sites based on species composition showed close clustering of Botanical arboretum, Laterite mixed shrubby, and Modified forest habitats (Fig. 3C). However, Agriculture and Coastal habitats were very distinct. The Moist mixed deciduous and Semi evergreen habitats were much closure. A NMDS plot (stress = 0.09) based on spatial replication data showed that replicates from many habitats such as Coastal, Agriculture, Semi evergreen, and Mixed moist deciduous showed distinct clustering indicating more dissimilar species compositions among these habitats. Replicates from other habitats were more closure and overlapping possibly due to more similar species compositions (Fig. S3).

The NMDS (stress = 0.13) of butterfly species in relation to habitat showed that low-abundant species (especially singletons) are situated at the periphery of the plot, while more abundant species are at the center (Fig. 3D). More unevenly distributed species in relation to their abundance (such as *Idea malabarica*) are at the periphery of the plot.

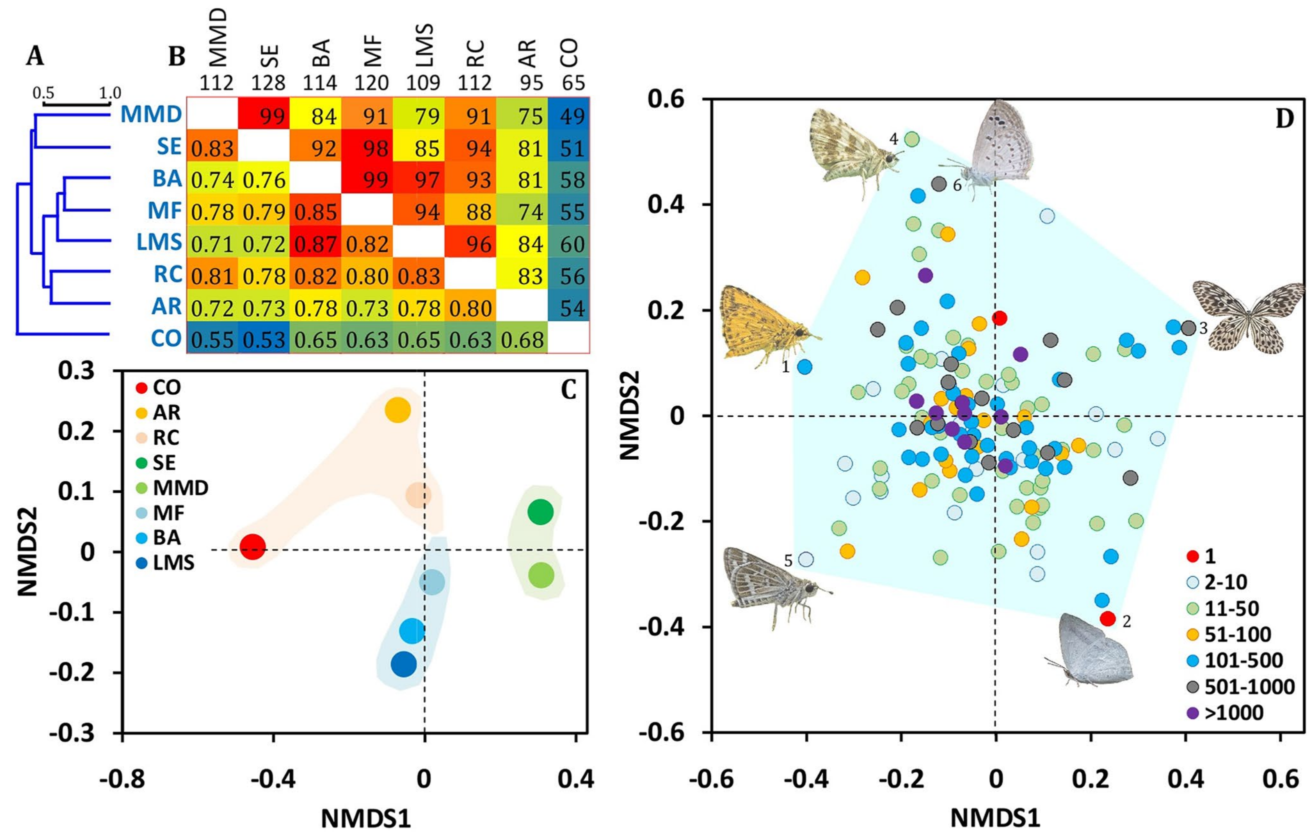

Fig. 3 Clustering of habitats and species. **A** Hierarchical clustering analysis of sites (based on Bray–Curtis dissimilarity) and **B** numbers (upper triangular matrix) and proportions (lower triangular matrix) of shared species among sites. The NMDS of **C** study sites (NMDS stress = 6.3E−5) based on species composition and **D** species (NMDS stress = 0.13) in relation to habitat. **C** Sites such as Coastal (CO) and Agriculture (AR) are far away from the center of the plot indicating distinct species composition possibly due to open habitats, while Modified forest (MF), Laterite mixed shrubby (LMS) and Botanical arboretum (BA) are closure likely due to similar and intermediate vegetation. See Fig. S3 for NMDS plot of habitat replicates. **D** Most (low-abundant) species are situated at the periphery of the plot (many points are not visible due to overlaps), while more abundant species are at the center. More unevenly distributed species in relation to their abundance [such as (3) *Idea malabarica*] are at the periphery of the plot. Flagged species in the figure are (1) *Ampittia dioscorides*, (2) *Curetis siva*, (3) *Idea malabarica*, (4) *Spialia galba*, (5) *Taractrocera maevius*, and (6) *Zizina otis*. The color of each point in D represents species abundance (classes: 1, 2–10, to > 1000 individuals)

Evenness of species across sites

The habitat equitability against the normalized abundance of species showed positive correlation (ρ = 0.622, p = 4.0E−20, correlation test, Fig. 4). For example, *Euploea* spp. and *Eurema hecabe* were some of the most abundant species which had high evenness across sites. On the other hand, most (n = 140, 77.9%) of the less abundant species (normalized abundance of less than 0.125—equivalent to presence in only one site) showed low (< 0.5) habitat equitability. However, it may be noted that some species such as *Papilio polytes* and *Phalanta phalantha* which were less abundant had high equitability indicating even presence across habitats. On the contrary, species which were abundant only in one site (for example, *Idea malabarica* in Semi evergreen habitat) or in a few sites (for example, *Acraea terpsicore* in Agriculture, Botanical arboretum, and Coastal habitats) showed, as expected, low habitat equitability values. Overall, hesperiids had low (normalized) abundance (0.02 ± 0.039, SEM) and lycaenids were less even (0.336 ± 0.026).

Conservation values of species versus local abundance and evenness

Figure 5A–D show the plots of conservation values of butterfly species (Kunte 2008) against the normalized abundance and habitat equitability, respectively. Overall, conservation value decreases (ρ = -0.353, p = 7.4E−6) against species abundance (Fig. 5A). Similarly, conservation value, as expected, had a significantly negative trend (ρ = -0.278, p = 0.0005) with habitat equitability (Fig. 5B). Within families, this trend is significant for Pieridae (p = 0.014), and Papilionidae (p = 0.048, Fig. 5C), but too weak and insignificant for Nymphalidae (p = 0.065), Hesperiidae (p = 0.35)

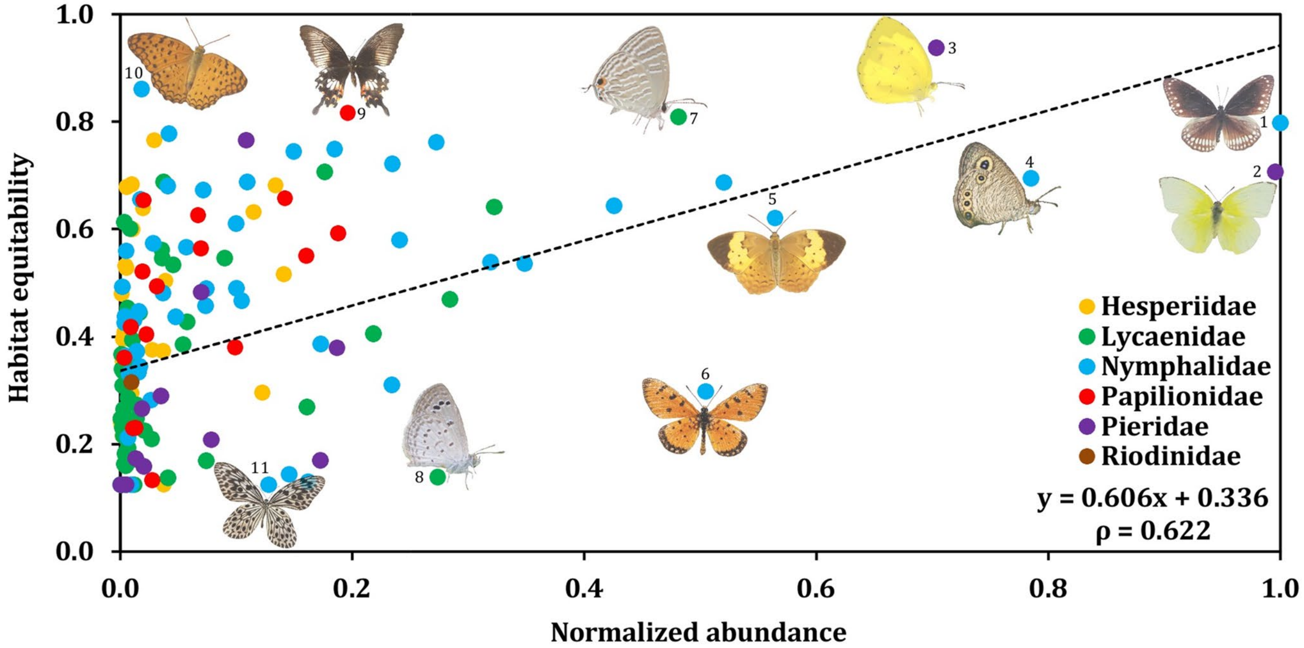

Fig. 4 Plot of habitat equitability versus normalized abundance. While evenness of butterfly species across sites showed a positive correlation with overall abundance, many species which were less abundant also had high evenness. Some species [such as (11) *Idea malabarica*, in forest ecosystem] which have specific niche had low evenness and might be sensitive to habitat disturbance. Overall, hesperiids were less abundant and lycaenids were less even. Flagged species in the figure are (1) *Euploea* spp., (2) *Catopsilia* spp., (3) *Eurema hecabe*, (4) *Ypthima huebneri*, (5) *Cupha erymanthis*, (6) *Acraea terpsicore*, (7) *Jamides celeno*, (8) *Zizina otis*, (9) *Papilio polytes*, (10) *Phalanta phalantha*, and (11) *Idea malabarica*

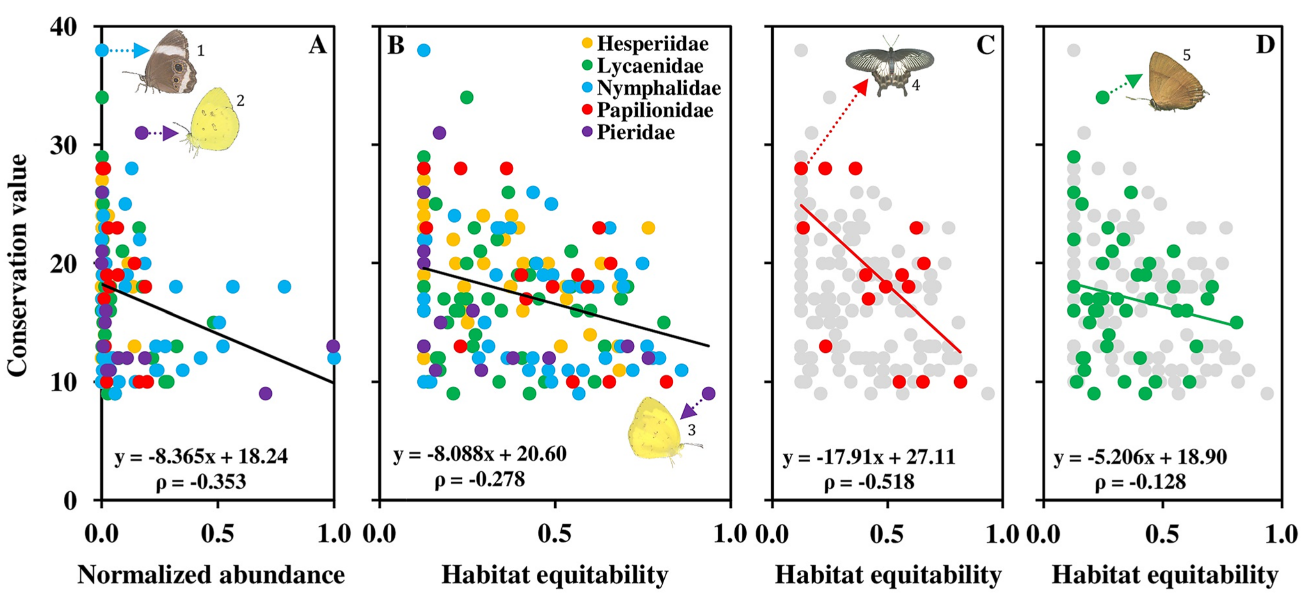

Fig. 5 Conservation value of butterfly species. Overall, conservation values of species are less if they are (A) more abundant and/or (B) even across habitats. Within families, the negative correlation trend of conservation value against evenness is significant for Pieridae (p = 0.014, correlation test) and (C) Papilionidae (p = 0.048), but too weak and insignificant for Nymphalidae (p = 0.065), Hesperiidae (p = 0.35), and (D) Lycaenidae (p = 0.41). Flagged species in the figure are (1) *Zipaetis saitis*, (2) *Eurema andersonii*, (3) *Eurema hecabe*, (4) *Pachliopta pandiyana*, and (5) *Rapala lankana*

and Lycaenidae ($p = 0.41$, Fig. 5D). Figure S4 shows the proportions of butterfly species in each of the eight landscapes with reference to global and local distribution data (Kunte 2008), and overall conservation values of eight habitats. The Coastal and Agriculture habitats had no species specific to Western Ghats, and had lower overall conservation values. On the other hand, Semi evergreen and Moist mixed deciduous habitats had higher proportions of species that had a restricted distribution, both global and local. As many as four species found in this study were listed in the schedule I [of the Wildlife (Protection) Act, 1972], 20 species in the schedule II, and six species in the schedule IV (Table S1) (Kunte 2008).

Indicator butterfly species

Using indicator value analysis (De Cáceres et al. 2010), a total of 103 indicator species ($p < 0.05$, permutation test) have been identified (Table S6). The proportion of indicator species ranged from 0.29 (Agriculture) and 0.31 (Coastal) to 0.52 (Semi evergreen) which best represented the individual habitats (De Cáceres et al. 2010; Sharma et al. 2020). However, only 22 single-site-specific indicator species have been found (Fig. S5), while remaining 81 species represented two or more sites (17 species in two sites [for example, *Neopithecops zalmora* in Mixed moist deciduous and Semi evergreen], 16 species for three sites, 13 species for four sites, 11 species each for five and six sites, and 13 species for seven sites (Table S6). Nine single-site-specific indicator species were found for Semi evergreen habitat, six for Coastal, but none found for Mixed moist deciduous and Rocky crop habitats (Fig. S5). Semi evergreen and Coastal sites seemed more distinct from each other and from other sites; and each might be important as a habitat that provides key resources for distinct assemblages of butterflies (Dennis et al. 2006). For example, *Idea malabarica* was only found in Semi evergreen habitat, while *Zizina otis* was found in most habitats but highly over-represented in Coastal habitat (Fig. 2E).

Common (host) plant species

A total of 194 common plant species (belonging to 74 families) were identified along the transects in eight study sites (Tables S2 and S5). Among those, only 30 species were found in Coastal while 103 species were found in Semi evergreen habitat. Of the 194 common plant species, at least 103 (53.1%) were known host plants (Kunte et al. 2021; Nitin et al. 2018) for at least 135 species (77.1%) of butterflies found in the present study. Site-wise proportion of host plants ranged from 0.52 (Semi evergreen) to a highest of 0.83 (Botanical arboretum) and the proportion of dependent butterfly species ranged from 0.38 (Coastal) to 0.68 (Semi evergreen). Altogether, there were 283 host-butterfly species pairs present, with lowest (29 pairs from 19 host- and 25 butterfly species) at Coastal and highest (129 pairs from 53 host- and 87 butterfly species) at Semi evergreen habitat. It is worth noting that there were numerous site-specific host-butterfly species pairs. For example, *Ampittia dioscorides* was an indicator species for Agriculture habitat that had a corresponding host plant *Oryza sativa*. Likewise, *Idea malabarica* at Semi evergreen habitat had *Aganosma cymosa* and *Parsonsia alboflavescens* as hosts, while *Phalanta alcippe* at Mixed moist deciduous (and Semi evergreen) habitat had *Rinorea bengalensis* as a host (Table S2). The *Cirrochroa thais* (which feeds on *Hydnocarpus pentandra*—an evergreen tree) was abundant in Botanical arboretum habitat that was being converted from degraded/open land to arboretum (in Pilikula Biological Park, Mangaluru) (see also Supplemental Information—results and discussion).

Discussion

Many studies have explored the occurrence patterns of butterfly communities in the Western Ghats (Padhye et al. 2012; and references therein). However, very few systematic studies have presented the abundance patterns (Kunte 1997), and studies from coastal plains of the Western Ghats are especially limited (Naik and Mustak 2016). Using a large transect survey sampling, in this study we have presented the occurrence and abundance patterns of butterfly communities of the coastal plains of the Western Ghats—a biodiversity rich hotspot but an ecologically sensitive region (Jitendra 2019).

The Western Ghats are home to 336 species of butterflies (Nitin et al. 2018). The pattern of occurrence of butterflies among different taxa found in this study are comparable with previous studies on butterflies of the Western Ghats region (Eswaran and Pramod 2005; Kunte et al. 1999; Mohandas and Remadevi 2019; Naik and Mustak 2016; Nayak et al. 2004; Nitin et al. 2018; Padhye et al. 2012). However, the present study provides a large dataset on the abundance patterns, and information on habitat-specific species compositions. The overall richness was lower in open habitats with less tree cover. Similar vegetation-specific patterns were observed across the Western Ghats (Kunte 1997, 2001; Kunte et al. 1999; Nayak et al. 2004; Padhye et al. 2006; 2012). The butterfly species composition was known to differ according to different habitat types, and was also greatly influenced by various physical and environmental factors like forest cover, habitat disturbance, altitude, rainfall, temperature, and plant diversity (Kasangaki et al. 2012). Butterfly community dynamics often depends on many environmental factors, and some amount of habitat disturbance including occasional small-area burning and habitat heterogeneity were known to be beneficial (Benton et al. 2003;

Bubová et al. 2015; Tews et al. 2004). This may be the reason for high diversity (despite low abundance) in some habitats (such as Rocky crop) that experienced occasional fire, and high diversity and abundance in heterogeneous/moderately disturbed (Modified forest) habitat. On the other hand, certain land management practices such as afforestation of open lands are known to negatively impact butterfly communities (Bubová et al. 2015). Anthropogenic disturbance/land use gradients and global warming have been shown to dynamically affect butterfly species and their range shifts along the elevation gradients of Eastern Himalaya (Acharya and Vijayan 2015; Chettri 2015; Dewan et al. 2019, 2021; Majumder et al. 2012) and Neotropical mountains (Molina-Martínez et al. 2016).

The biodiversity in the Western Ghats is facing intense pressure from anthropogenic activity, directly and indirectly (Bawa et al. 2007). For example, agricultural intensification and associated land-use changes are reducing the Indian summer monsoon rainfall (Niyogi et al. 2010). Butterflies are sensitive and react rapidly to climate and habitat changes (Kunte 1997; Molina-Martínez et al. 2016; Padhye et al. 2006; Warren et al. 2001; White and Kerr 2007). Agricultural intensification inevitably drives butterfly decline (Habel et al. 2019), but low intensity agriculture is shown to support high butterfly diversity (Loos et al. 2014). In the present work, the abundance of butterflies in Agriculture habitat was found to be more than some other more wooded habitats. Butterflies communities are shown to respond differently along the agro-ecosystem-forest gradients in the Eastern Himalaya, and play a complementary role to the protected areas in butterfly conservation (Majumder et al. 2012; Sharma et al. 2020). Agro-ecosystems such as coffee plantations are important repositories of butterflies (Dolia et al. 2007). Therefore, while the Western Ghats will inevitably undergo further agro-ecological transformations (Jitendra 2019), it should be kept low intensity (Loos et al. 2014) and heterogeneous (Benton et al. 2003; Weibull et al. 2003) to support biodiversity including butterflies. Human-modified ecosystems both inside and outside the protected areas (Chettri 2015; Chettri et al. 2018; Sharma et al. 2020), including remnant forests (Anand et al. 2010), as well as agricultural (Munyuli 2013) and urban landscapes (Kuussaari et al. 2021; Paul and Sulthana 2020) are key repositories of butterflies for conservation (Bonebrake et al. 2010; Francesconi et al. 2013; Gardner et al. 2009).

In general, the occurrence/abundance patterns of butterflies, apart from habitat preference and various other factors, can be linked to their host plants (see also Supplemental Information—results and discussion and Table S2) (Ferrer-Paris et al. 2013). This knowledge can be helpful for the conservation of butterfly communities of the Western Ghats (Nitin et al. 2018). Except for a few species, such as *Idea malabarica* which might have specific niche requirements, conservation of most butterfly species might be limited by the availability of host plants (Dolia et al. 2007; Kunte 2001; Nitin et al. 2018). As a result, it could be possible to modify a habitat, for example from degraded to woody/forest, to partly restore butterfly communities. Even patchy restorations of forests are shown to sustain biodiversity and help in conservation (Anand et al. 2010). It is important to retain diverse habitats that harbour unique species compositions/abundances for the conservation of butterflies in the Western Ghats. In addition, as indicator species need not be unique to a site (De Cáceres et al. 2010), the habitat specific butterfly community structure can serve as a good indicator and is useful for the long term monitoring of the state/health of the ecosystem. Therefore, regular surveys of overall dominance patterns of species can be used to monitor the health of this anthropogenically active but ecologically sensitive region.

To comment on the limitations of this study, while there were a few studies on species composition (with very less emphasis on abundance) of butterfly communities in the larger geographical area of the Western Ghats (Nayak et al. 2004; Padhye et al. 2012), current work was restricted to the coastal plains of the Western Ghats. Further, while others have attempted to identify the drivers of occurrence and abundance (Dolia et al. 2007; Kunte 2001; Shahabuddin and Ali 2001), our emphasis was on habitat-specific abundance patterns of butterfly communities. Neither have we studied the temporal changes in the butterfly communities (Nieto-Sánchez et al. 2015; Wepprich et al. 2019). We are currently working on the seasonal dynamics of butterflies of the Western Ghats in relation to climate and conservation.

Conclusions

We surveyed the butterfly taxon in eight heterogeneous landscapes/sites of the coastal plains and foothills of the Western Ghats, and counted 43,118 individuals and 175 species. Large differences in the diversity and species-specific abundance patterns of butterflies were observed among sites ranging from the coastal to semi-evergreen habitats, with intermediate patterns in agricultural and other habitats. Several site-specific and shared species were identified using indicator value analysis. There were also habitat-specific relationship with the presence of common host-plants. As even common butterfly species showed quite distinct ecological niches based on their habitat-specific abundance, they can be helpful as indicator species to monitor the community dynamics. Our study gives an important baseline data on the butterfly communities of Western Ghats for their conservation as well as for the future monitoring of this ecologically sensitive region.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This work is in compliance with ethical standards. No ethical clearance was necessary. No butterflies were killed or collected in this study.

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