

Influence of forest structure on butterfly diversity in tropical deciduous forests of Sambalpur district, Odisha, India

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Abstract

Butterflies are important ecological indicators in tropical forest ecosystems, where vegetation structure and habitat heterogeneity strongly influence their diversity and distribution. The present study assessed butterfly diversity, community assemblages, and seasonal variation across three forest habitat types in the Sambalpur district of western Odisha, India, namely Reserve Open Forest (S1), Reserve Dense Forest (S2), and Reserve Plantation Forest (S3). Six transects, with two established in each habitat type, were surveyed monthly from January to December 2022 using the Pollard Walk method. A total of 98 butterfly species belonging to six families were recorded, with Nymphalidae being the dominant family. Among the studied habitats, Reserve Dense Forest (S2) supported the highest butterfly diversity, with higher Shannon ($^1D = 54.75$) and inverse Simpson diversity values ($^2D = 36.57$), followed by Reserve Plantation Forest (S3) and Reserve Open Forest (S1). Rarefaction curves approached asymptotic levels across all habitats, indicating adequate sampling completeness. Butterfly species richness and abundance differed significantly among forest habitats (Kruskal–Wallis test, $p < 0.05$), highlighting the influence of vegetation complexity and habitat structure on butterfly assemblages. Seasonal variation was also significant, with the highest richness and abundance observed during the post-monsoon period. The findings demonstrate that dense and structurally heterogeneous forest habitats support more diverse butterfly communities in tropical deciduous landscapes. This study provides baseline information on butterfly diversity in western Odisha and emphasizes the importance of integrating butterfly-based monitoring into forest management and landscape-level conservation planning under increasing land-use change and climate variability in eastern India.

Introduction

Biodiversity underpins human well-being, supporting ecosystem stability, livelihood security, and essential ecological processes (Zhang et al. 2022). Tropical forests, in particular, represent some of the most biologically rich systems on Earth (Lewis et al. 2015). In India, these forests contribute substantially to global biodiversity, harboring nearly 7.8% of the world's species (<https://www.cbd.int/countries/profile?country=in>) within about 25.17% of the country's total forest cover (FSI 2023). Among the various forest types, tropical dry deciduous forests (TDDFs) form a dominant component, accounting for roughly 38–42% of India's forested landscape (FSI 2023). Despite their ecological importance, these forests remain under persistent pressure from human activities such as agricultural expansion, mining, and fragmentation. Such disturbances not only reduce forest cover but also alter microclimatic conditions, thereby threatening the integrity and functioning of these ecosystems (Mahata et al. 2023).

Butterflies are an important component of tropical forest ecosystems and play a significant role in maintaining ecological balance. In the tropical deciduous forests of India, they act as pollinators, herbivores, and a vital food source for many birds, reptiles, and other insects. Their close relationship with host plants also supports plant reproduction and genetic diversity (Ghazanfar et al. 2016). Moreover, butterflies are highly sensitive to environmental disturbances, habitat degradation, and

climatic fluctuations, making them reliable bioindicators of ecosystem health and environmental change. Changes in butterfly diversity and abundance often reflect the health and quality of an ecosystem. Butterflies also contribute to habitat restoration by enhancing pollination and supporting natural vegetation regeneration in disturbed forest areas (Legal et al. 2020). Furthermore, many butterfly species are considered umbrella species, as conserving their habitats indirectly protects numerous other organisms sharing the same ecosystem (New 1997).

Forest structure plays a crucial role in shaping butterfly diversity and distribution in tropical deciduous forests. Variations in canopy cover, vegetation density, tree composition, and understory complexity influence the availability of host plants, nectar resources, light intensity, and microclimatic conditions that are essential for butterfly survival and reproduction (Mahata et al. 2023). Structurally diverse forests generally support higher butterfly richness by providing a wide range of ecological niches and breeding habitats (Mahata et al. 2024). In contrast, habitat fragmentation, deforestation, and changes in forest composition can alter these microhabitats and negatively affect butterfly communities (Brückmann et al. 2010). Therefore, understanding the relationship between forest structure and butterfly diversity is important for evaluating habitat quality and developing effective conservation and forest management strategies in tropical deciduous ecosystems.

India is recognized as one of the global biodiversity hotspots for butterflies, supporting nearly 1,500 species due to its wide range of climatic conditions and diverse forest ecosystems (Kunte 2000; Kehimkar 2016; Sidhu 2023). Tropical deciduous forests, which dominate large parts of central and eastern India, provide suitable habitats for numerous butterfly species because of their rich vegetation structure, host plant availability, and seasonal resource dynamics (Tiple 2011; Mahata et al. 2020; Mahata and Palita 2023). In Odisha, however, comprehensive studies on butterfly diversity across different forest habitats remain limited, with most research concentrated in protected areas, coastal and Eastern Ghats region. Several studies have highlighted the rich butterfly diversity of the state. For instance, Paria et al. (2018) documented 95 butterfly species from the Kuldiha Wildlife Sanctuary, emphasizing the ecological importance of mixed tropical deciduous forests and heterogeneous landscapes. Similarly, Boruah et al. (2018) recorded 135 species from the Manchabandha and Budhikhamari Reserve Forests of Mayurbhanj district, while Payra et al. (2016) reported 136 species from the Similipal Biosphere Reserve, with Nymphalidae being the dominant family. More recently, Palei and Rath (2014) documented 101 butterfly species from Sunabeda Wildlife Sanctuary. Studies from the Eastern Ghats of Odisha have also shown that butterfly diversity varies considerably among different forest habitats, including dense forests, open forests, and riparian forests, where habitat-specific microclimatic conditions strongly influence species composition and assemblages (Mahata et al. 2024). Mahata and Palita, (2023) recorded 148 butterfly species from the Koraput district of Odisha in the Eastern Ghats and reported that riparian forests supported comparatively higher butterfly diversity due to favourable environmental conditions and resource availability (Mahata et al. 2023).

At the same time, increasing anthropogenic disturbances, including agroforestry expansion, habitat fragmentation, and forest modification, are affecting butterfly diversity and abundance in tropical forest

landscapes (Mahata et al. 2019). Bacha and Lenka, (2023) reported moderate butterfly diversity in agroforestry habitats of southern and western Odisha, indicating that altered habitats can support butterfly communities but may not sustain specialist forest-dependent species.

Although some butterfly studies have been conducted in the Sambalpur region, information remains limited largely to semi-urban landscapes. For instance, Bacha et al. (2023) documented 75 butterfly species from the semi-urban Sambalpur University campus at Burla town, representing 53 genera and 17 subfamilies belonging to six families.

Despite these studies, information on butterfly community structure across different forest habitat types in western Odisha remains poorly understood. In particular, no systematic study has examined how butterfly species richness, abundance, and assemblages vary among Reserve Open Forests, Reserve Dense Forests, and Reserve Plantation Forests in the Sambalpur district. Moreover, the influence of seasonal variation, especially during monsoon, summer, and post-monsoon periods, on butterfly assemblages and habitat associations has not been adequately explored. Such information is essential for understanding landscape connectivity, habitat heterogeneity, and ecological dynamics of butterfly communities in tropical deciduous forest ecosystems.

Therefore, the present study was undertaken to assess butterfly diversity and community assemblages across different forest habitat types in the Sambalpur district of western Odisha. In addition, the study examines seasonal variation in butterfly communities during the summer, monsoon, and post-monsoon periods to better understand temporal patterns in species distribution and habitat utilization. The specific objectives of the study were: (i) to evaluate butterfly diversity and abundance in Reserve Open Forest, Reserve Dense Forest, and Reserve Plantation Forest habitats; (ii) to compare species assemblages and community composition among these forest habitat types; and (iii) to analyse seasonal variation in butterfly assemblage across different habitats.

It was hypothesized that butterfly diversity and species richness would vary significantly among forest habitat types due to differences in vegetation structure, habitat complexity, and resource availability. It was further expected that structurally complex and heterogeneous dense forest habitats would support greater butterfly diversity and distinct community assemblages compared to open and plantation forests. Additionally, butterfly community composition and abundance were anticipated to exhibit marked seasonal variation, with higher richness and abundance during the post-monsoon seasons owing to favourable microclimatic conditions and increased availability of host and nectar plants.

Material and methods

Study area

The study was conducted in Sambalpur district of western Odisha, eastern India, located between 20°40'–22°11' N and 82°39'–85°15' E, covering an area of 6,702 km², of which approximately 50.18% (3,363.30 km²) is under forest cover, forming an ecologically important part of the central Mahanadi

River basin. The landscape comprises three major physiographic units: forest-clad hills in the north, an undulating plateau in the south-east, and riverine valleys and plains associated with the Mahanadi and its tributaries, with elevations ranging from 146 to 288.6 m above mean sea level. The district is characterised by a hot tropical monsoonal climate with extreme summer temperatures (mean maximum up to $\sim 46^{\circ}\text{C}$ in April–May), a pronounced southwest monsoon contributing nearly 90% of the annual rainfall (long-term mean $\sim 1,495$ mm), and a mild to cool winter with occasional cold waves lowering minimum temperatures to $\sim 7.6^{\circ}\text{C}$. Relative humidity remains high (80–90%) during the monsoon and declines substantially during winter. Soils are heterogeneous, dominated by Aqualfs, Ustalfs, Ochrepts and associated lithic and alluvial complexes, while the underlying geology comprises Archaean and Cuddapah formations enriched with economically important minerals such as graphite, coal, iron ore and alluvial gold (Sethi 2011). Vegetation falls largely within the Dry Peninsular Sal Forest (C1c) subtype of the Northern Tropical Dry Deciduous Forests (5B), where Sal (*Shorea robusta*) occurs in fragmented and edaphically constrained patches and is frequently replaced by dry mixed deciduous communities dominated by *Cleistanthus collinus*, *Anogeissus latifolia*, *Diospyros melanoxylon* and *Odina wodier*, interspersed with extensive stands of *Dendrocalamus strictus*, particularly over granitic and gneissic substrates. Moist tendencies in the south-eastern parts support semi-evergreen elements, while economically and ecologically significant tree species such as *Tectona grandis*, *Pterocarpus marsupium*, *Terminalia spp.*, *Gmelina arborea*, *Bombax ceiba*, *Butea monosperma* and *Schleichera oleosa* contribute to structural complexity and resource heterogeneity (Champion and Seth 1968). This mosaic of physiography, climate, soils and vegetation creates diverse habitat conditions that support rich wildlife assemblages and high ecological variability typical of central Indian deciduous forest landscapes.

Three forest types were selected for the study based on forest cover characteristics and management regimes of the State Forest Department: Reserve Open Forest (S1; $21^{\circ}44'53''$ N, $84^{\circ}26'56''$ E; 292 m a.s.l.), Reserve Dense Forest (S2; $21^{\circ}23'39''$ N, $84^{\circ}04'52''$ E; 228 m a.s.l.) and Reserve Plantation Forest (S3; $21^{\circ}04'53''$ N, $84^{\circ}18'12''$ E 238 m a.s.l.) (Fig. 1). Detailed descriptions of the study sites are provided in Table 1.

Table 1

Habitat characteristics of the studied tropical deciduous forest sites—Reserve Open Forest (S1), Reserve Dense Forest (S2), and Reserve Plantation Forest (S3)—in Sambalpur district, Odisha, India.

Habitat characteristics	Reserve Open Forest (S1)	Reserve Dense Forest (S2)	Reserve Plantation Forest (S3)
GPS Location	21°44'53"N 84°26'56"E	21°23'39"N 84°04'52"E	21°04'53"N 84°18'12"E
Elevation (m)	292m	228m	238m
Area (km ²)			
Dominated trees	<i>Shorea robusta</i> , <i>Terminalia tomentosa</i> , <i>Buchanania lanzan</i> , <i>Anogeissus latifolia</i> , <i>Cleistanthus collinus</i> , <i>Diospyros melanoxylon</i> , <i>Syzigium cumini</i> , <i>Pterocarpus marsupium</i> , <i>Madhuca latifolia</i> , <i>Soymida febrifuga</i> .	<i>Chloroxylon swietenia</i> , <i>Buchanania lanzan</i> , <i>Cleistanthus collinus</i> , <i>Lannea coromandelica</i> , <i>Diospyros melanoxylon</i> , <i>Anogeissus latifolia</i> , <i>Pterocarpus marsupium</i> , <i>Lagerstroemia parviflora</i> , <i>Boswellia serrata</i> , <i>Emblica officinalis</i> .	<i>Cleistanthus collinus</i> , <i>Pterocarpus marsupium</i> , <i>Anogeissus latifolia</i> , <i>Buchanania lanzan</i> , <i>Garuga pinnata</i> , <i>Madhuca latifolia</i> , <i>Terminalia tomentosa</i> , <i>Diospyros melanoxylon</i> , <i>Bridelia retusa</i> , <i>Stereospermum suaveolens</i> .
Dominated shrubs	<i>Ardisia solanacea</i> , <i>Grewia hirsuta</i> , <i>Helicteres isora</i> , <i>Zyziphus oenoplia</i> , <i>Cenchrus pedicellatus</i>	<i>Ardisia solanacea</i> , <i>Grewia hirsuta</i> , <i>Cipadessa baccifera</i> , <i>Clerodendrum viscosum</i> , <i>Woodfordia fruticosa</i> , <i>Helicteres isora</i> , <i>Zyziphus oenoplia</i> , <i>Cenchrus pedicellatus</i>	<i>Terminalia tomentosa</i> , <i>Buchanania lanzan</i> , <i>Pterocarpus marsupium</i> , <i>Lannea coromandelica</i> , <i>Diospyros melanoxylon</i> , <i>Garuga pinnata</i> , <i>Helicteres isora</i> , <i>Cenchrus pedicellatus</i>
Dominated grasses	<i>Arundinella setosa</i> , <i>Thysanolaena maxima</i> , <i>Themeda triandra</i> , <i>Elueusine indica</i>	<i>Cyperus iria</i> <i>Cyperus difformis</i> <i>Themeda triandra</i> , <i>Eulaliopsis binita</i> , <i>Curex intumescens</i> , <i>Elueusine indica</i>	<i>Curex intumescens</i> , <i>Elueusine indica</i>

Habitat characteristics	Reserve Open Forest (S1)	Reserve Dense Forest (S2)	Reserve Plantation Forest (S3)
Disturbance level	High HI, High G	Least HI Least G	Moderate HI, Least G

Disturbance levels were categorised based on an anthropogenic activity scale reflecting the frequency of human encounters (HI) and grazing intensity (G) recorded during each transect count: least (HI = 0–1 encounters), moderate (HI = 3–4 encounters), and high (HI = 8–10 encounters) (Mahata et al. 2018).

Butterfly sampling

A total of six transects were established across the study area, comprising two transects within each of the three sampling sites, with a single 500 m transect laid in each forest habitat. These transects were surveyed once every month over a one-year period from January to December 2022. Butterfly abundance was assessed using the Pollard Walk method (Pollard 1977), with minor modifications to suit local habitat conditions. During each survey, butterflies were recorded within an imaginary sampling window extending 2.5 m on either side of the transect line and 5 m ahead of and above the observer.

Observations were conducted between 08:00 and 11:00 h, maintaining a uniform walking speed so that each 500 m transect was completed in approximately 60 minutes. All surveys were undertaken by two observers working together, with one person focusing on detecting and identifying butterflies while the other systematically recorded the observations. Species identification was primarily based on direct visual sightings supported by photographic documentation, using standard butterfly field guides (Kunte 2000; Kehimkar 2016) and the taxonomic nomenclature followed by <https://www.ifoundbutterflies.org/>.

Data analysis

Species richness (S) and relative abundance (RA) are commonly applied quantitative indicators used to describe the biological diversity of ecological communities. Species richness refers to the total number of species present within a given community, whereas relative abundance represents the proportion, expressed as a percentage, of individuals of each species in relation to the total number of individuals across all species (Magurran 2004). To evaluate butterfly diversity across different forest types, we employed rarefaction and extrapolation methods based on a reference sample and expressed diversity using Hill numbers, namely species richness ($q = 0$), the Shannon diversity index ($q = 1$), and the inverse Simpson index ($q = 2$). Extrapolation analyses were conducted using the “iNEXT” package in R, extending the sample size to twice that of the reference sample for each survey site. In addition, rarefaction and extrapolation curves, along with estimates of sample coverage (SC), were generated using the same package to assess the completeness and robustness of the diversity estimates (Hsieh et al. 2016).

Differences in species richness and abundance among sampling sites (S1, S2, and S3) were analysed using the Kruskal–Wallis test, as sample sizes were small ($n = 12$ observations per site) and data did not meet parametric assumptions. When overall tests were significant, post-hoc pairwise comparisons were

conducted using Wilcoxon rank-sum tests with Benjamini–Hochberg correction to control the false discovery rate (Zuur et al. 2007; Hollander et al. 2014).

Seasonal variation in species richness and abundance was examined across four seasons (Winter, Summer, Monsoon, and Post-monsoon), with nine observations per season. Given the limited sample size ($n = 9$), non-parametric statistical approaches were applied. Seasonal differences were assessed using the Kruskal–Wallis test, followed by pairwise Wilcoxon rank-sum tests with Benjamini–Hochberg adjustment (Zuur et al. 2007; Hollander et al. 2014).

In addition to p-values, effect sizes (r) were calculated for all pairwise Wilcoxon comparisons to quantify the magnitude of differences and support ecological interpretation. Effect sizes were interpreted following conventional thresholds (small: $r < 0.30$; medium: $0.30–0.49$; large: ≥ 0.50) (Cohen 2013). Results are presented as boxplots, with sample sizes indicated below each box; significant pairwise differences are denoted by asterisks, and overall Kruskal–Wallis p-values are shown above each plot.

All statistical analyses were performed in R (version 4.5.1; R Core Team, 2025) using the packages *ggplot2*, *ggpubr*, *cowplot* and *rstatix*.

Result

Species assemblages

A total of 98 butterfly species belonging to six families were documented during the study period. The family Nymphalidae was the most dominant and species-rich group, accounting for 37 species, indicating its strong representation within the study area. This was followed by Lycaenidae with 23 species and Pieridae with 14 species. Moderate species richness was recorded for Hesperidae (12 species) and Papilionidae (11 species). In contrast, Riodinidae was the least represented family, with only a single species recorded. Four species recorded during the survey— *Pachliopta hector*, *Papilio clytia*, *Hypolimnas misippus*, and *Tanaecia lepidea* —are listed under the schedules of the Wildlife (Protection) Act, 1972. *Catopsilia pomona* (Fabricius, 1775), *Euploea core*, *Mycalesis perseus*, and *Eurema hecabe* were the most common species, contributing more than 5% to this tropical forest ecosystem. A few widespread butterfly species were commonly recorded in sites S2 and S3, whereas the open forest site (S1) supported all generalist species occurring across the study area. *Tagiades gana* and *Troides helena* were primarily associated with the dense forest site (S2) (Table 2).

Table 2

Relative abundance of butterfly species recorded in tropical deciduous forest sites—Reserve Open Forest (S1), Reserve Dense Forest (S2), and Reserve Plantation Forest (S3)—in Sambalpur district, Odisha, India.

Butterfly Species	Relative abundance (RA)			Total assemblage
	S1	S2	S3	
Subfamily: HesperIIDae				
1. <i>Caprona ransonnetti</i> (Felder, 1868)	0	0.62	0.23	0.34
2. <i>Hasora chromus</i> (Cramer, [1780])	0.24	0.28	0.09	0.2
3. <i>Hasora vitta</i> (Buutler,1870)	0.24	0.97	0.79	0.73
4. <i>Iambrix salsala</i> (Moore, [1866])	0.08	0.28	0.23	0.21
5. <i>Notocrypta curvifascia</i> (C. & R. Felder, 1862)	0.24	0.37	0.12	0.25
6. <i>Papilio paris</i> (Linnaeus, 1758)	0.96	0.37	0.47	0.54
7. <i>Parnara guttatus</i> (Bremer and Grey, [1852])	0.56	1.06	1.11	0.95
8. <i>Pseudoboro bevani</i> (Moore,1878)	0.16	0.28	1.28	0.58
9. <i>Sarangesa dasahara</i> (Moore, [1865])	0.56	0.18	0.17	0.27
10. <i>Spialia galba</i> (Fabricius, 1793)	0.12	0.88	0.23	0.48
11. <i>Tagiades gana</i> (Moore, [1866])	0	0.09	0	0.04
12. <i>Udaspes folus</i> (Cramer, [1775])	0.2	0.76	3.43	1.52
Subfamily: Lycaenidae				
13. <i>Acytolepis puspa</i> (Horsfield, [1828])	4.46	2.65	1.02	2.55
14. <i>Amblypodia anita</i> Hewitson, 1862	0.72	1.29	0.84	1
15. <i>Arhopala amantes</i> (Hewitson, 1862)	0.68	1.11	3.67	1.86
16. <i>Castalius rosimon</i> (Fabricius, 1775)	1.23	1.64	1.83	1.6
17. <i>Catochrysops strabo</i> (Fabricius, 1793)	0.04	0.67	0.7	0.52
18. <i>Chilades lajus</i> (Stoll, [1780])	4.74	0.95	2.39	2.35
19. <i>Euchrysops cnejus</i> (Fabricius, 1798)	1.95	2.4	2.01	2.16
20. <i>Euploea klugii</i> (Moore, 1858)	0	0.18	0.03	0.09
21. <i>Everes hugelii</i> (Gistel, 1857)	0.52	0.65	0.76	0.65
22. <i>Everes lacturnus</i> (Godart, [1824])	0.44	0.25	0.99	0.54
23. <i>Freyeria trochylus</i> (Freyer, 1845)	0.24	0.46	0.26	0.34

Butterfly Species	Relative abundance (RA)			Total assemblage
	S1	S2	S3	
24. <i>Jamides bochus</i> (Stoll, [1782])	1.07	2.28	2.33	2
25. <i>Jamides celeno</i> (Cramer, [1775])	0.08	0.37	3.38	1.3
26. <i>Lampides boeticus</i> (Linnaeus, 1767)	0.12	0.09	1.6	0.6
27. <i>Loxura atymnus</i> (Stoll, 1780)	0.12	0.28	0.15	0.19
28. <i>Pseudozizeeria maha</i> (Kollar, [1844])	0.08	0.23	0.12	0.16
29. <i>Rathinda amor</i> (Fabricius, 1775)	0.08	0.14	0	0.08
30. <i>Spindasis vulcanus</i> (Fabricius, 1775)	0.2	0.88	0.15	0.47
31. <i>Tajuria jehana</i> Moore, [1884]	0.04	0.09	0.06	0.07
32. <i>Tarucus nara</i> (Kollar, 1848)	0.32	0.21	0.52	0.34
33. <i>Udara akasa</i> (Horsfield, [1828])	0.24	0.65	0.47	0.49
34. <i>Zizina otis</i> (Fabricius, 1787)	0.96	1.18	0.12	0.77
35. <i>Zizula hylax</i> (Fabricius, 1775)	0.28	0.83	0.81	0.69
Subfamily: <i>Nymphalidae</i>				
36. <i>Acraea terpsicore</i> (Linnaeus, 1758)	1.23	2.31	3.2	2.34
37. <i>Ariadne ariadne</i> (Linnaeus, 1763)	3.14	1.31	1.34	1.77
38. <i>Ariadne merione</i> (Cramer, [1777])	0.08	0.09	0.12	0.1
39. <i>Athyma perius perius</i> (Linnaeus, 1758)	1.23	0.25	0.87	0.7
40. <i>Charaxes bernardus</i> (Fabricius, 1793)	0.32	0.3	0.09	0.23
41. <i>Charaxes solon</i> (Fabricius, 1793)	0.16	0.07	0	0.07
42. <i>Chliaria othona</i> (Hewitson, 1865)	0.08	0.3	0.15	0.19
43. <i>Danaus chrysippus</i> (Linnaeus, 1758)	2.67	2.07	2.18	2.26
44. <i>Danaus genutia</i> (Cramer, [1779])	0.56	0.39	0.12	0.34
45. <i>Elymnias hypermnestra</i> (Linnaeus, 1763)	0.08	0.28	0.2	0.2
46. <i>Euploea core</i> (Cramer, [1780])	2.87	5.99	5.7	5.13
47. <i>Euploea midamus</i> (Linnaeus, 1758)	0.08	0.37	0.32	0.28
48. <i>Hypolimnas misippus</i> (Linnaeus, 1764)	0.12	0.67	0.12	0.35
49. <i>Junonia almana</i> (Linnaeus, 1758)	1.39	1.8	1.37	1.56

Butterfly Species	Relative abundance (RA)			Total assemblage
	S1	S2	S3	
50. <i>Junonia atlites</i> (Linnaeus, 1763)	3.11	1.64	4.31	2.89
51. <i>Junonia hierta</i> (Fabricius, 1798)	0.28	0.39	0.47	0.39
52. <i>Junonia iphita</i> (Cramer, [1779])	1.99	1.78	2.1	1.93
53. <i>Junonia lemonias</i> (Linnaeus, 1758)	0.28	3.25	1.43	1.92
54. <i>Junonia orithya</i> (Linnaeus, 1758)	0.2	0.23	0.09	0.17
55. <i>Kallima inachus</i> (Doyère, 1840)	0.4	1.64	2.01	1.46
56. <i>Melanitis leda</i> (Linnaeus, 1758)	3.14	0.88	0.61	1.34
57. <i>Moduza procris</i> (Cramer, [1777])	0.12	0.25	0.26	0.22
58. <i>Mycalesis mineus</i> (Linnaeus, 1758)	3.94	3.02	0.67	2.46
59. <i>Mycalesis perseus</i> (Fabricius, 1775)	5.49	5.03	1.11	3.83
60. <i>Neptis ananta</i> Moore, [1858]	0.08	0.3	0.55	0.33
61. <i>Neptis hylas</i> (Linnaeus, 1758)	1.35	1.59	1.89	1.63
62. <i>Neptis Sappho</i> (Pallas,1771	0	0.14	0.03	0.07
63. <i>Parantica aglea</i> (Stoll, [1782])	0.08	0.14	0.09	0.11
64. <i>Phalanta phalantha</i> (Drury, [1773])	0.28	0.23	0.06	0.18
65. <i>Polyura athamas</i> (Drury,1773)	0.08	0.07	0.06	0.07
66. <i>Symphaedra nais</i> (Forster, 1771)	1.59	2.28	1.54	1.87
67. <i>Tanaecia lepidea</i> (Butler, 1868)	0.6	0.65	0.67	0.64
68. <i>Telicota colon</i> (Fabricius, 1775)	0	0.23	0.03	0.11
69. <i>Tirumala limniace</i> (Cramer, [1775])	0.16	0.71	0.29	0.44
70. <i>Vanessa cardui</i> (Linnaeus, 1758)	0.4	0.05	0.52	0.29
71. <i>Vanessa cardui</i> (Linnaeus,1758)	0.08	0.12	0.09	0.1
72. <i>Ypthima huebneri</i> Kirby, 1871	0.32	0.46	0.29	0.37
<i>Subfamily: Papilionidae</i>				
73. <i>Graphium agamemnon</i> (Linnaeus, 1758)	0.08	0.39	0.09	0.21
74. <i>Graphium nomius</i> (Esper,1793)	0	0.18	0.12	0.12
75. <i>Melanitis lphedima</i> (Cramer, 1780)	5.65	2.51	3.06	3.46

Butterfly Species	Relative abundance (RA)			Total assemblage
	S1	S2	S3	
76. <i>Pachliopta aristolochiae</i> (Fabricius, 1775)	0.48	1.06	0.41	0.7
77. <i>Pachliopta hector</i> (Linnaeus, 1758)	0.2	0.25	0.26	0.24
78. <i>Papilio clytia</i> Linnaeus, 1758	0.68	0.23	0.2	0.33
79. <i>Papilio crino</i> Fabricius, 1793	0.32	0.81	0.32	0.52
80. <i>Papilio demoleus</i> Linnaeus, 1758	3.18	2.1	2.42	2.47
81. <i>Papilio polymnestor</i> Cramer, 1775	0.28	0.58	0.38	0.44
82. <i>Papilio polytes</i> Linnaeus, 1758	0.76	0.39	0.32	0.46
83. <i>Troides helena</i> (Linnaeus, 1758)	0	0.05	0	0.02
Subfamily: Pieridae				
84. <i>Appias olferna</i> Swinhoe, 1890	0.16	0.71	0.41	0.48
85. <i>Belenois aurota</i> (Fabricius, 1793)	0.48	0.74	0.47	0.58
86. <i>Catopsilia pomona</i> (Fabricius, 1775)	8.16	5.79	3.9	5.74
87. <i>Catopsilia pyranthe</i> (Linnaeus, 1758)	0.64	0.35	0.12	0.34
88. <i>Cepora nerissa</i> (Fabricius, 1775)	0.4	0.37	0.35	0.37
89. <i>Delias eucharis</i> (Drury, 1773)	0.48	0.48	0.58	0.52
90. <i>Eurema andersonii</i> (Moore, 1886)	0.16	0.85	0.26	0.49
91. <i>Eurema blanda</i> (Boisduval, 1836)	0.56	0.39	1.11	0.67
92. <i>Eurema hecabe</i> (Linnaeus, 1758)	5.18	5.6	5.24	5.38
93. <i>Eurema laeta</i> (Boisduval, 1836)	7.76	6.45	8.56	7.48
94. <i>Gandaca harina</i> (Horsfield, [1829])	0.84	0.35	1.05	0.7
95. <i>Ixias marianne</i> (Cramer, [1779])	0.04	0.39	0.35	0.29
96. <i>Leptosia nina</i> (Fabricius, 1793)	2.91	1.38	2.1	1.99
97. <i>Pareronia hippia</i> (Fabricius, 1787)	0.44	0.32	0.47	0.4
Subfamily: Riodinidae				
98. <i>Abisara echerius</i> (Stoll, [1790])	0.28	0.41	0.23	0.32

The reference sample from the dense forest site (S2) exhibited the highest diversity, with elevated values of the Shannon index ($^1D = 54.75$) and inverse Simpson index ($^2D = 36.57$), and a total of 98 taxa. This

was followed by site S3 ($^0D = 94$, $^1D = 49.13$, $^2D = 33.65$) and site S1 ($^0D = 91$, $^1D = 40.75$, $^2D = 27.26$). Rarefaction curves for species richness (^0D) approached an asymptote after an initial steep increase across all forest types, indicating high sampling completeness and limited accumulation of additional species with increased sampling effort (Fig. 2). This pattern was further supported by sample coverage estimates, which were highest for S2 (SC = 100%), followed by S3 (SC = 99.91%) and S1 (SC = 99.88%) at $q = 0$

The relative abundance of species was highest for the Nymphalidae family (38.34), followed by Pieridae (25.41), Lycaenidae (20.28), Papilionidae (8.97), Hesperidae (6.12), and least for the Riodinidae family (0.32). The highest relative abundance recorded in S2 (42.17), followed by S3 (33.40), and lowest in S1 (24.42) (Table 2).

Spatial heterogeneity

Species richness

Species richness showed significant variation among the forest sites (Kruskal–Wallis test: $\chi^2 = 12.82$, $df = 2$, $p < 0.01$) (Fig. 3a). Median (IQR) species richness was 34.5 (15.5) at S1, 56.6 (12.75) at S2, and 46.5 (11.75) at S3. Pairwise comparisons using Wilcoxon rank-sum tests with Benjamini–Hochberg adjustment revealed that site S2 supported significantly different species richness compared with both S1 and S3 ($p < 0.05$). In contrast, no significant difference was observed between S1 and S3 ($p > 0.05$). Effect size estimates (r) were large ($r \geq 0.50$) for all comparisons involving site S2, indicating pronounced differences relative to the other sites (Table 3).

Abundance

Species abundance varied significantly among the forest sites (Kruskal–Wallis test: $\chi^2 = 7.78$, $df = 2$, $p < 0.05$) (Fig. 3b). Median (IQR) species abundance was 154.5 (187.8) at S1, 359 (172.25) at S2, and 239 (183.5) at S3. Post-hoc pairwise Wilcoxon rank-sum tests with Benjamini–Hochberg correction showed a significant difference in species abundance between sites S1 and S2 ($p < 0.05$). In contrast, comparisons between S1 and S3 and between S2 and S3 were not statistically significant ($p > 0.05$). Effect size estimates (r) indicated a large effect ($r \geq 0.50$) for the S1–S2 comparison, reflecting a pronounced difference in abundance between these two sites (Table 3).

Table 3

Results of post-hoc pairwise comparisons of species richness and abundance among forest sites based on Wilcoxon rank-sum tests with Benjamini–Hochberg correction (BH).

Seasonal comparison	W statistic		Adjusted p-value (BH)		Effect size (r)	
	Richness	Abundance	Richness	Abundance	Richness	Abundance
S1 vs S2	16.5	28	0.004	0.03	0.65	0.57
S1 vs S3	42.5	43	0.093	0.128	0.34	0.01
S2 vs S3	114.5	99	0.023	0.128	0.50	0.66

Seasonal variation

Species richness

Species richness varied significantly among seasons (Kruskal–Wallis test: $\chi^2 = 16.29$, $df = 3$, $p < 0.05$), indicating the presence of pronounced seasonal differences (Fig. 4a). Median (IQR) richness was 48 (14) in winter, 26 (13) in summer, 45 (15) in monsoon, and 65 (20) in post-monsoon. Post-hoc pairwise comparisons using the Wilcoxon rank-sum test with Benjamini–Hochberg adjustment identified significant contrasts between specific seasonal pairs. Richness during the post-monsoon season differed significantly from that observed in summer, monsoon, and winter ($p < 0.05$). A significant difference was also detected between summer and monsoon seasons, whereas winter did not differ significantly from either summer or monsoon ($p > 0.05$). Effect size estimates (r) revealed large effects ($r \geq 0.50$) for comparisons involving the post-monsoon season and for the summer–monsoon contrast, while winter–monsoon and winter–summer comparisons exhibited small effects ($r < 0.30$) (Table 4). Collectively, these findings indicate that seasonal variation in species richness is both statistically significant and ecologically meaningful, with the most pronounced differences associated with the post-monsoon period.

Abundance

Species abundance exhibited significant seasonal variation (Kruskal–Wallis test: $\chi^2 = 19.75$, $df = 3$, $p < 0.05$) (Fig. 4b). Median (IQR) abundance was 279 (140) in winter, 150 (97) in summer, 273 (75) in monsoon, and 435 (60) in post-monsoon. Post-hoc pairwise Wilcoxon comparisons indicated that abundance during the post-monsoon season differed significantly from that recorded in summer, monsoon, and winter ($p < 0.05$). Additional significant differences were detected between summer and winter, as well as between summer and monsoon, whereas no significant difference was observed between monsoon and winter seasons. Effect size analysis revealed large effects ($r \geq 0.50$) for all seasonal comparisons except monsoon versus winter (Table 4). The magnitude of these effect sizes underscores the pronounced influence of seasonal dynamics on species abundance, with peak values occurring during biologically favourable periods, particularly the post-monsoon season.

Table 4

Results of post-hoc pairwise comparisons of species richness among seasons based on Wilcoxon rank-sum tests with Benjamini–Hochberg correction (BH).

Seasonal comparison	W statistic		Adjusted p-value (BH)		Effect size (r)	
	Richness	Abundance	Richness	Abundance	Richness	Abundance
Winter vs Summer	63	68	0.06	0.02	0.47	0.57
Winter vs Monsoon	36.5	41	0.76	1.00	0.08	0.01
Winter vs Post-monsoon	14	9	0.03	0.01	0.55	0.66
Summer vs Monsoon	12.5	15	0.03	0.03	0.58	0.53
Summer vs Post-monsoon	3	0	0.01	0.00	0.78	0.84
Monsoon vs Post-monsoon	13	8	0.03	0.01	0.57	0.68

Discussion

The documentation of 98 butterfly species belonging to six families underscores the high conservation value of the study area within the Indian biogeographic context. As observed in many forested landscapes across peninsular India, Nymphalidae emerged as the most dominant family, followed by Lycaenidae, Pieridae, Papilionidae, Hesperidae, and Riodinidae. Similar family-level dominance patterns have been consistently reported from the Eastern Ghats and other tropical forest systems in India, where nymphalids often constitute the largest proportion of butterfly assemblages due to their broad ecological amplitude, diverse larval host plant range, and adaptability to varying habitat conditions (Kunte 2000; Mahata et al. 2019, 2020; Mahata 2021; Mahata and Palita 2023).

The observed dominance of Nymphalidae in the present study is likely attributable to both its taxonomic breadth and evolutionary flexibility. As the largest butterfly family, Nymphalidae exhibits a wide range of ecological strategies, including well-developed mimicry systems that are particularly prominent in tropical environments and are thought to enhance survival under diverse ecological pressures (Resh and Carde 2009). Such evolutionary adaptations may contribute to the successful establishment and persistence of nymphalid species across a variety of habitat types. In addition, the high diversity of plant species characteristic of tropical forest ecosystems provides an extensive array of larval host plants, supporting both monophagous and polyphagous butterfly species (Bonebrake et al. 2010; Tiple et al. 2011). This broad availability of host resources is likely to favor nymphalid butterflies, which are known for their flexible larval feeding habits and ability to exploit a wide spectrum of host plants. Together, these ecological and evolutionary factors help explain the consistent dominance of Nymphalidae observed in tropical butterfly assemblages, including those of eastern and central Indian landscapes.

The substantial representation of Pieridae and Lycaenidae further reflects the heterogeneous vegetation structure typical of Eastern Ghats landscapes, which include a mosaic of dry deciduous forests, scrublands, and open forest patches. Such habitat heterogeneity is known to enhance butterfly richness by supporting both generalist species and host-plant-specific taxa (Kehimkar 2016; Mahata et al. 2023, 2024). In contrast, the comparatively lower richness of Papilionidae, Hesperidae, and Riodinidae is consistent with previous studies from the Eastern Ghats and central India, where these families are often represented by fewer species due to their greater dependence on specific forest microhabitats, larval host plants, or limited detectability during standard survey periods (Mohapatra et al. 2012; Tiple 2012; Mahata and Palita 2023). Overall, the observed family composition suggests that the study area supports a diverse and ecologically functional butterfly community, reinforcing the importance of Eastern Ghats forests for regional butterfly conservation.

The occurrence of several legally protected butterfly species highlights the conservation significance of the present study area. Four species recorded during the survey—*Pachliopta hector*, *Papilio clytia*, *Hypolimnas misippus*, and *Tanaecia lepidea*—are listed under the schedules of the Wildlife (Protection) Act, 1972. The presence of these conservation-priority taxa indicates that the study landscape provides suitable habitat conditions for species of high legal and ecological importance. Such findings emphasize the role of these forest habitats as effective refuges for protected butterflies and underline the necessity of maintaining habitat integrity through informed forest management practices and long-term conservation planning.

Community composition was further characterized by a small number of dominant and widespread species, including *Catopsilia pomona*, *Euploea core*, *Mycalesis perseus*, and *Eurema hecabe*, each contributing more than 5% to the total assemblage. These species are known for their ecological flexibility, broad larval host plant use, and tolerance of varying habitat conditions, traits that allow them to thrive across a range of tropical forest environments (Mahata et al. 2019). Their dominance is typical of butterfly communities in human-influenced or heterogeneous landscapes and often reflects the availability of common host plants and open canopy conditions (Mahata et al. 2019; Mahata and Palita 2023).

Spatial patterns in species distribution revealed clear habitat associations. Widespread species were frequently recorded in both S2 and S3, indicating resource continuity between these habitats, while the open forest site (S1) supported all generalist taxa, likely due to greater floral availability and favourable microclimatic conditions (Mahata et al. 2023). In contrast, habitat-specialist species such as *Tagiades gana* and *Troides helena* were largely restricted to the dense forest site (S2), highlighting the importance of structurally complex and less-disturbed forests in supporting specialist and conservation-sensitive taxa. Collectively, these findings demonstrate that maintaining a mosaic of habitat types—particularly dense and mature forest patches—is essential for sustaining both common and legally protected butterfly species within tropical forest landscapes.

The higher diversity observed in the dense forest site (S2), as indicated by elevated Shannon (^1D) and inverse Simpson (^2D) indices, suggests a more even and structurally complex butterfly community compared with the other forest types. Dense forests typically support greater habitat heterogeneity, stable microclimatic conditions, and a higher diversity of larval host plants and nectar resources, all of which promote species coexistence and reduce dominance by a few taxa (Álvarez et al. 2024). Although species richness (^0D) was relatively comparable among sites, the lower ^1D and ^2D values at S1 and S3 indicate assemblages increasingly dominated by common, generalist species, a pattern frequently reported from more open or disturbed habitats (Vu et al. 2015).

The rarefaction curves approaching asymptotes across all forest types, together with near-complete sample coverage, confirm that sampling effort was sufficient to capture the majority of species present and that the observed diversity patterns reflect true ecological differences rather than methodological artefacts (Chao et al. 2014). Collectively, these results highlight the critical role of dense forest habitats in sustaining both high species diversity and community evenness, reinforcing their importance for butterfly conservation within tropical forest landscapes (New 2013).

The significant differences in species richness among forest sites highlight the strong influence of habitat structure and quality on butterfly community composition. The consistently higher richness recorded at dense forest (S2), coupled with large effect sizes, suggests that this site provides a greater diversity of ecological niches, likely driven by higher vegetation heterogeneity, stable microclimatic conditions, and a wider range of larval host plants and nectar resources (Hamer et al. 2003). The lack of significant difference between S1 and S3 indicates that these habitats may offer broadly similar resource availability or experience comparable levels of disturbance, resulting in comparable richness patterns. Similar site-specific effects of forest structure on butterfly richness have been widely documented in tropical forest landscapes (Mahata et al. 2023).

Patterns of species abundance further reinforce the importance of habitat quality, with the pronounced difference between S1 and S2 suggesting that population sizes respond more sensitively to local environmental conditions than richness alone. Higher abundance at S2 may reflect favourable microhabitats that enhance survivorship and reproductive success, whereas the lower abundance at S1 could be associated with greater exposure, reduced canopy cover, or seasonal resource limitation (Pollard and Yates 1993). The absence of significant abundance differences involving S3 implies that, although species presence may be comparable, population densities are moderated by local habitat conditions. Together, these findings demonstrate that dense or structurally complex forest habitats play a key role in sustaining both high species richness and robust butterfly populations, emphasizing their conservation value within managed tropical forest landscapes (Kunte 1997).

The maximum butterfly diversity was found in undisturbed forests (S2), than relatively more disturbed plantation (S3) and open (S4). In contrast, the open forest (S1) showed the least diversity may be due more disturbance in the form of logging grazing ant anthropogenic pressure. Generally, tropical forest butterfly communities exhibit stable patterns, indicating ecological interactions and niche partitioning

(Young, 1972). Butterfly habitat selection is greatly influenced by natural forest edges; certain species favour these locations because of the resources they offer and the opportunities they have to interact with other species (Nowicki et

The pronounced seasonal differences in species richness and abundance underscore the strong influence of climatic seasonality on butterfly communities in tropical forest ecosystems. The consistently higher richness observed during the post-monsoon period suggests that this season provides optimal conditions for butterfly persistence, likely driven by increased vegetation growth, higher availability of larval host plants, and abundant floral resources following monsoonal rainfall (Robinson et al. 2012). The large effect sizes associated with post-monsoon comparisons further indicate that these seasonal shifts are ecologically substantial rather than merely statistically detectable.

The significant contrast between summer and monsoon seasons highlights the transitional nature of resource availability and microclimatic conditions. During summer, elevated temperatures and reduced moisture can limit larval survival and adult activity, whereas the onset of the monsoon improves habitat conditions but may also impose constraints due to heavy rainfall and reduced flight activity (Mahata et al. 2024). The lack of strong differences involving winter, reflected by small effect sizes, suggests relatively stable or uniformly reduced resource conditions across seasons, resulting in comparable levels of species richness.

Seasonal patterns in abundance closely mirrored those of richness, with peak abundance recorded during the post-monsoon season. This period likely supports synchronized emergence and higher survivorship of multiple species, leading to marked increases in population size. In contrast, the absence of significant differences between monsoon and winter indicates that population densities remain constrained during less favourable periods. Overall, these findings demonstrate that seasonal dynamics play a pivotal role in structuring butterfly communities, emphasizing the importance of post-monsoon conditions for maintaining high diversity and abundance in tropical forest landscapes (Koli et al. 2025).

Conclusion

This study provides clear evidence that butterfly diversity in the central Mahanadi River basin of eastern India is strongly shaped by habitat quality, forest structure, and seasonal dynamics. Undisturbed dense forests emerged as key reservoirs of both high species richness and community evenness, highlighting the importance of structural complexity, microclimatic stability, and diverse larval host and nectar resources in sustaining butterfly assemblages. In contrast, open and more disturbed forest habitats supported lower diversity and abundance, reflecting the negative influence of logging, grazing, and other anthropogenic pressures. Seasonal patterns further revealed that post-monsoon conditions are particularly critical, supporting peak richness and abundance, likely due to enhanced vegetation growth and resource availability.

The occurrence of legally protected and habitat-specialist species underscores the conservation value of the study landscape and its role as a regional refuge for butterfly biodiversity. Together, these findings

emphasize that the maintenance of intact dense forest patches, regulation of anthropogenic disturbances, and consideration of seasonal ecological processes are key determinants for conserving butterfly diversity in the central Mahanadi River basin. Integrating butterfly-focused monitoring into forest management and landscape-level conservation planning will be essential for safeguarding these ecologically sensitive indicators under ongoing land-use change and climate variability in eastern India.

Declarations

Conflict of interest

The authors declare no conflict of interest.

Ethical approval

The study involved non-invasive field surveys and was conducted in accordance with local biodiversity and conservation guidelines. No protected or endangered species were intentionally harmed during the study.

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Author Contribution

Basudev Bacha: Conceptualization, Methodology, Investigation, Data Curation, Resources, Writing - Review and Editing. Ayusmita Naik: Software, Formal analysis, Writing - Review and Editing, Visualization. Anirban Mahata: Conceptualization, Methodology, Software, Validation, Formal analysis, Writing - Original Draft, Writing - Review and Editing, Supervision.

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Data Availability

Data will be made available on request.

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Figures

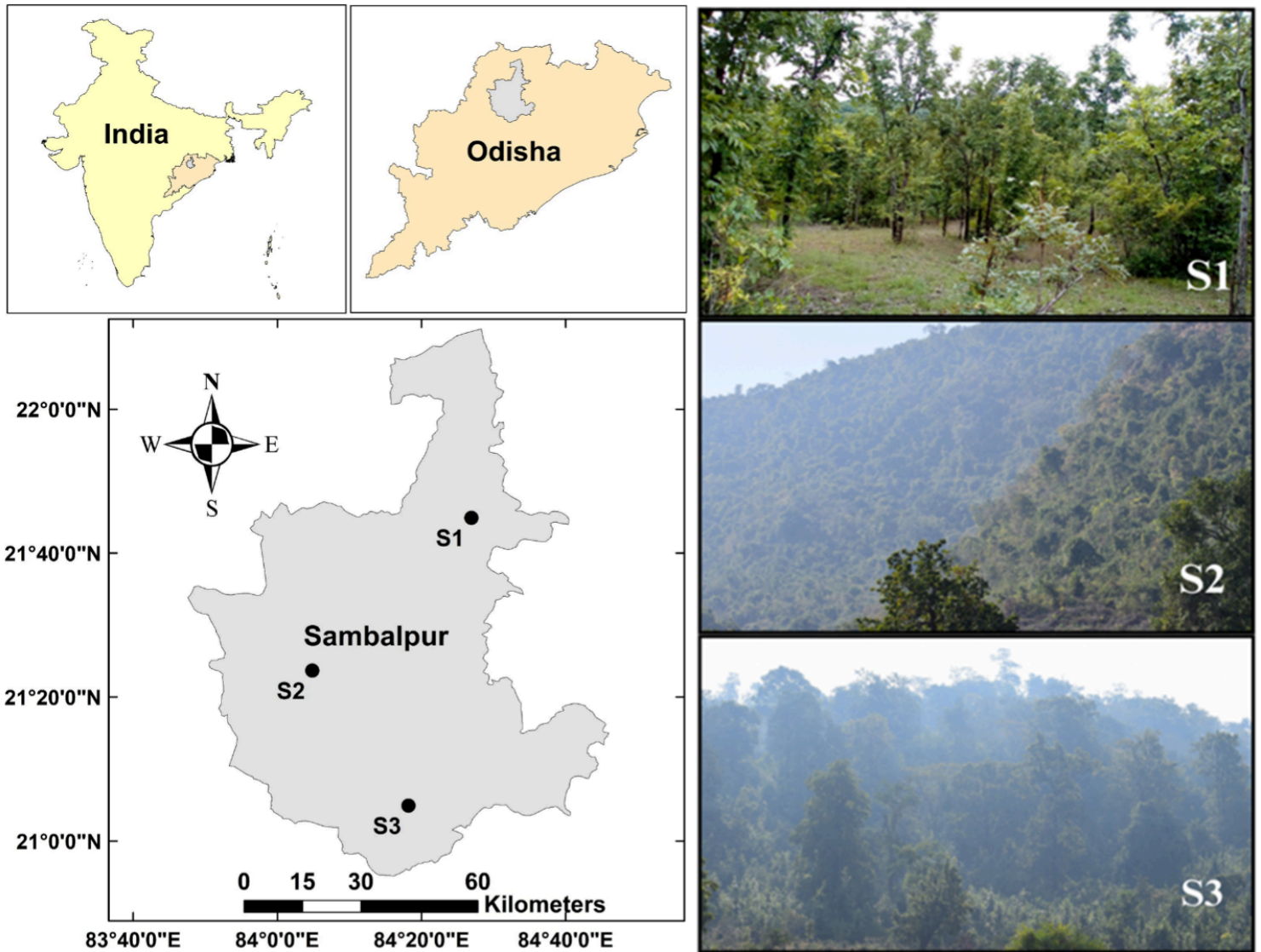


Figure 1

Map of the study area showing the locations of the three sampling sites in Sambalpur district, Odisha, India: Reserve Open Forest (S1), Reserve Dense Forest (S2), and Reserve Plantation Forest (S3). The inset on the right illustrates the corresponding forest habitat types investigated in the study.

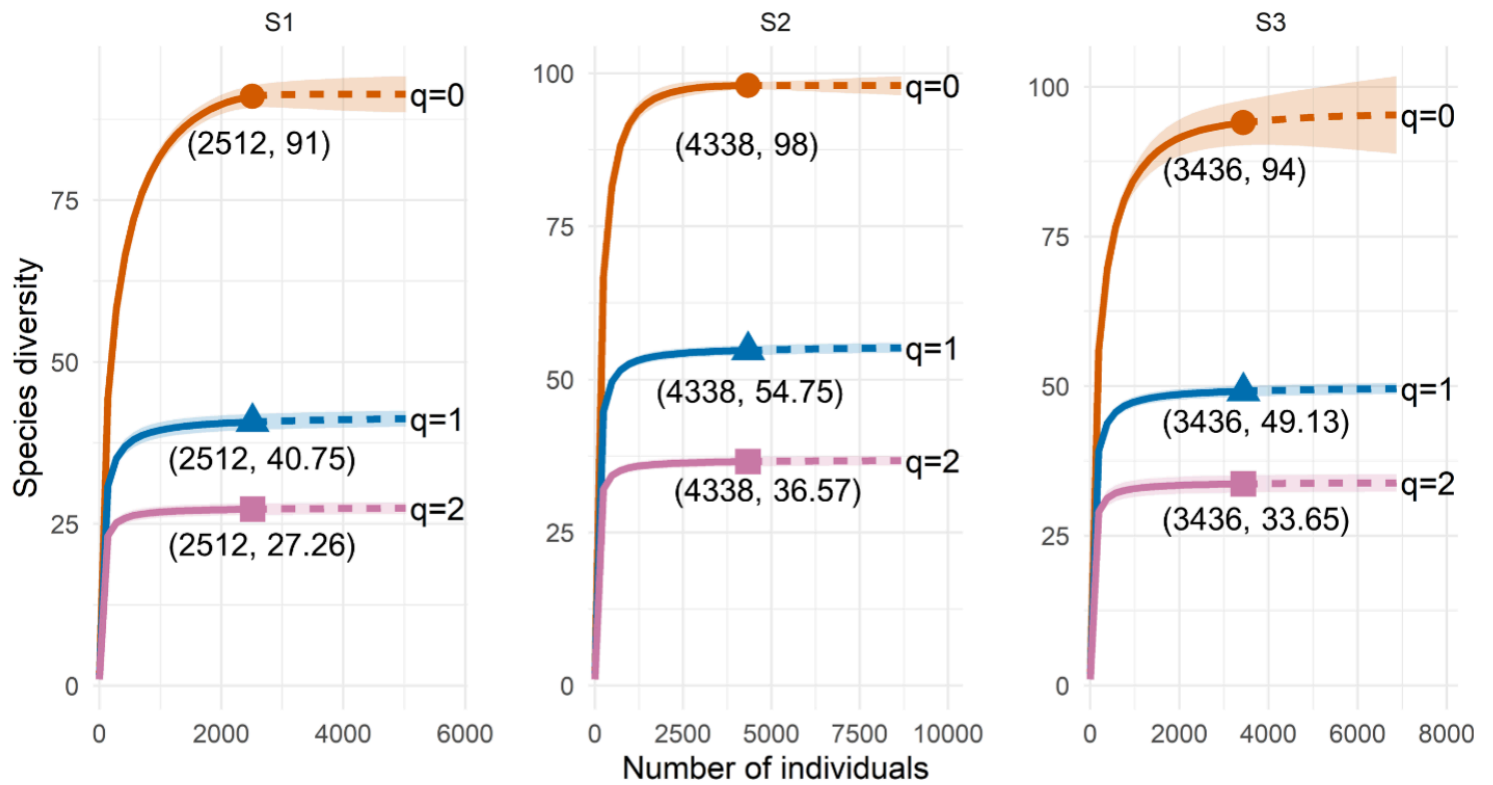


Figure 2

Rarefaction (interpolation) and extrapolation curves illustrating species richness ($q = 0$), Shannon diversity ($q = 1$), and inverse Simpson diversity ($q = 2$) for the three study sites (S1, S2, and S3). Solid lines indicate rarefaction curves, while dotted lines show extrapolations extending to twice the reference sample size. Values in parentheses represent the sample size and observed Hill numbers for the reference samples, and dashed lines mark the corresponding biodiversity estimates. Shaded areas denote 95% confidence intervals generated using bootstrap resampling (999 iterations).

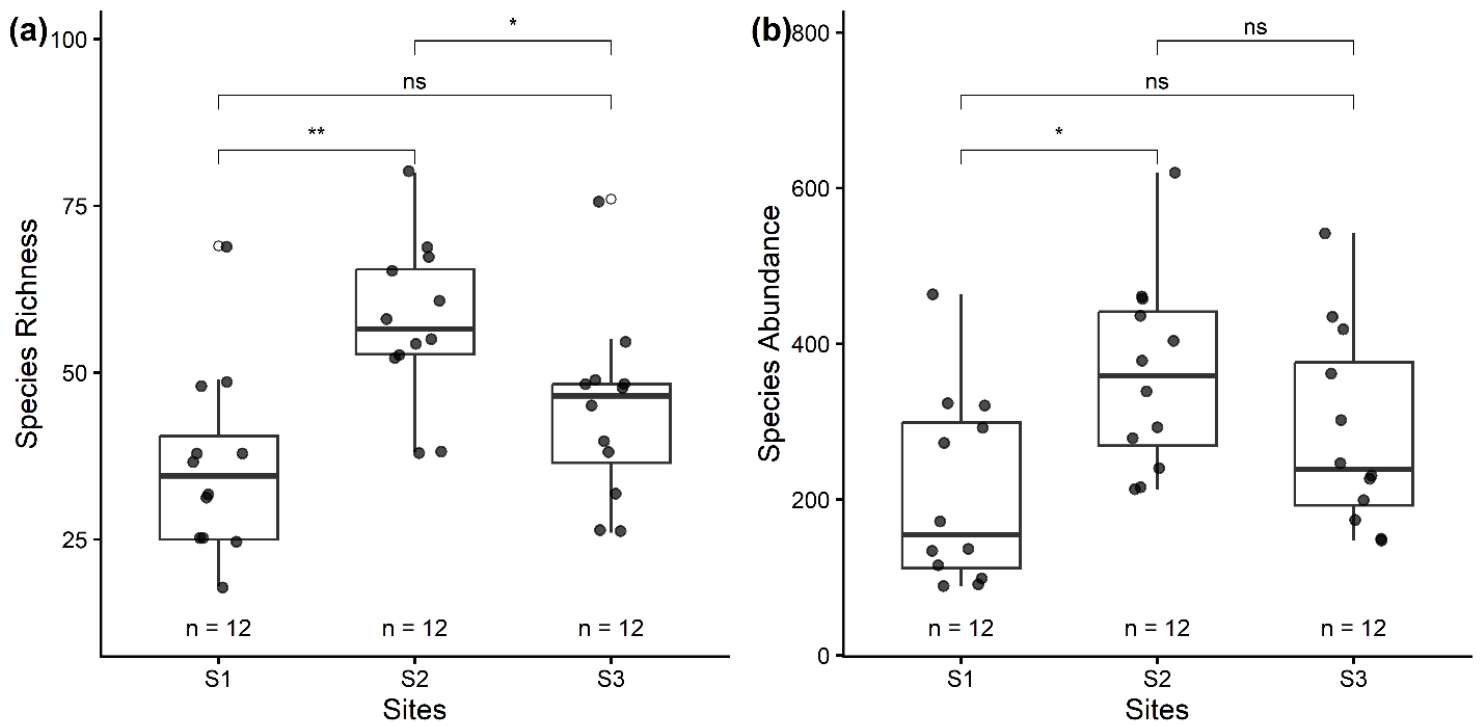


Figure 3

Site-wise variation in (a) species richness and (b) species abundance across the study area. Boxplots show median values, interquartile ranges, and $1.5 \times$ IQR whiskers; points represent individual sampling observations. Sample sizes for each season are shown below the boxes. Pairwise differences among seasons were tested using Wilcoxon rank-sum tests, with significance indicated by asterisks ($p < 0.05$, $p < 0.01$).

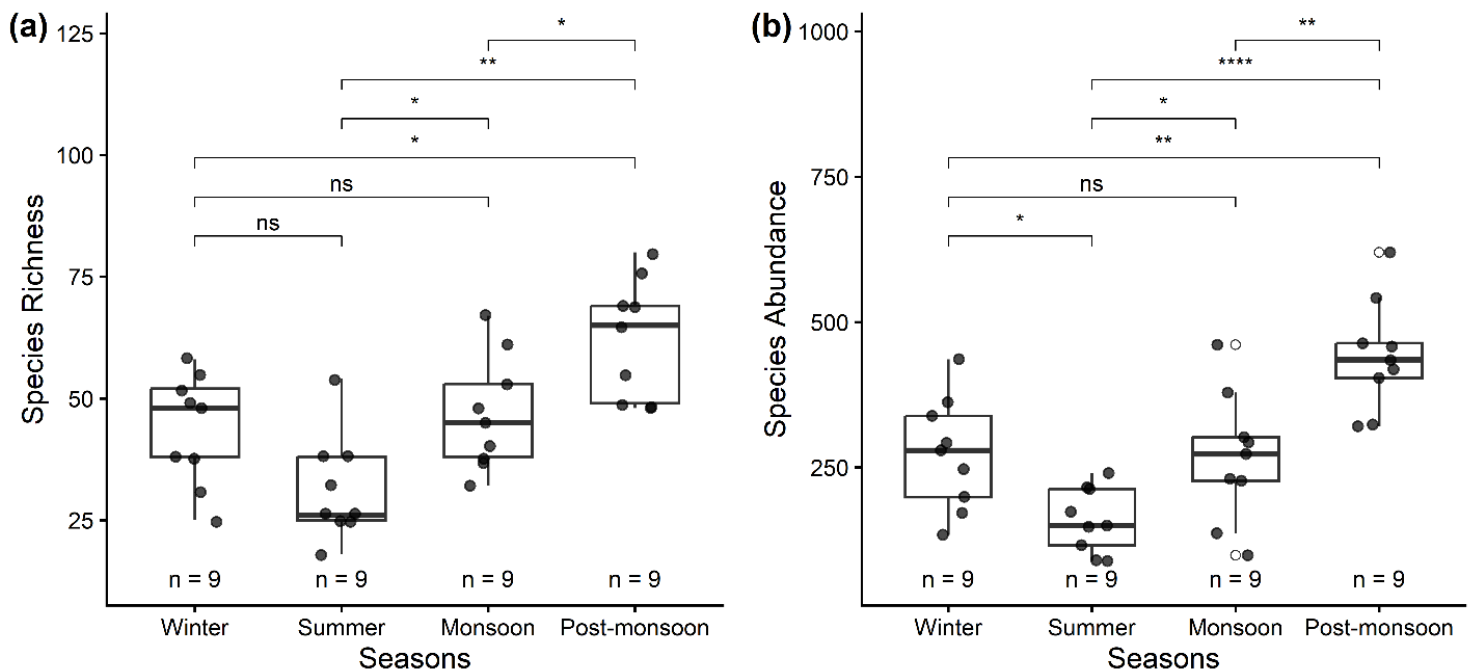


Figure 4

Seasonal variation in (a) species richness and (b) species abundance across the study area. Boxplots show median values, interquartile ranges, and 1.5× IQR whiskers; points represent individual sampling observations. Sample sizes for each season are shown below the boxes. Pairwise differences among seasons were tested using Wilcoxon rank-sum tests, with significance indicated by asterisks ($p < 0.05$, $p < 0.01$, $p < 0.0001$).