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Research Article

Vegetation determines butterfly diversity and composition across the Arabuko-Sokoke coastal forest in Kenya, a tropical biodiversity hotspot

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Abstract

Community structures, including butterfly diversity, are shaped by both biotic and abiotic factors, with forest type exerting a significant influence. The Arabuko Sokoke Forest (ASF), the largest remaining coastal forest fragment in Kenya and East Africa, is rich in biodiversity and endemic species. Given its varied forest types, ASF provides a unique opportunity to examine how these differences affect butterfly community structure. This study aims to investigate how vegetation diversity and structure influence butterfly community structures and species richness within ASF. We conducted butterfly and woody plant surveys during the dry season across four distinct forest types in ASF: *Cynometra* forest, *Brachystegia* woodland, mixed forest and the forest edge. Butterfly populations were sampled using transects measuring 10 m × 100 m and woody plant species were surveyed along overlapping transects. A total of 6,050 butterfly individuals were recorded, representing 86 species across 38 genera and five families. The woody vegetation comprised 178 species, belonging to 78 genera and 34 families. Significant differences in butterfly species abundance were observed across the forest types, though no significant differences were found in species richness. Beta diversity analyses revealed consistently high community dissimilarity across all forest types, driven predominantly by balanced variation in species abundances rather than nestedness. *Brachystegia* forest exhibited the highest total beta diversity, while forest edge exhibited the lowest. This indicates that species turnover, rather than richness differences, is the primary mechanism structuring butterfly communities at the landscape scale in Arabuko Sokoke Forest. Butterfly species diversity showed a strong correlation with plant species diversity. Additionally, butterfly wingspan size varied significantly amongst forest types. Our findings underscore the crucial role of natural plant forest diversity in supporting butterfly diversity and highlight the synergistic functions of the mixed forest and *Brachystegia* forest as key habitats. There is need for conservation strategies that account for multiple dimensions of biodiversity. While mixed forest serves as a reservoir of high species richness and abundance, *Brachystegia* forest offers critical value through their contribution to beta diversity at the landscape level. These results highlight the fundamental importance of conservation efforts directed to protect high plant diversity and structural heterogeneity to provide a broad spectrum of ecological niches and habitat connectivity for butterflies. Such strategies will enhance butterfly diversity and contribute to effective conservation in fragmented forests and especially in Arabuko Sokoke Forest.

Key Words

Arabuko Sokoke Forest, butterfly diversity, community structure, forest edge, habitat connectivity, habitat quality, plant species, species co-occurrence, tropical forests

Introduction

Community structures are shaped by the interplay of biotic and abiotic factors, with forest type exerting a significant influence on butterfly diversity. Different forest types can significantly impact butterfly diversity through changes in microclimate, resource availability, plant diversity and vegetation structure (Schweitzer and Dey 2011). Butterflies are widely regarded as effective bioindicators of habitat quality and ecosystem health due to their sensitivity to environmental changes and close associations with host plants and microhabitats (Bouyer et al. 2007; Dobson 2012). Their community composition and species richness often reflect underlying patterns in vegetation diversity and structure, making them valuable for monitoring biodiversity responses to habitat variation.

Globally, an estimated 18,000 butterfly species have been documented, with approximately 3,600 species occurring in Africa and around 870 recorded in Kenya (Larsen 1991). The Arabuko-Sokoke Forest alone supports over 300 of Kenya's butterfly species, highlighting its significance as a global biodiversity hotspot (Ayiemba 1995; ASF Management Team 2002). It is estimated that, globally, approximately 90% of butterflies are found in tropical areas, but their ecological role is less studied than in temperate regions, which also applies to vegetation studies (Bonebrake et al. 2010; see Fungomeli et al. (2020b)).

Butterflies play a crucial role as a biogeographical and ecological indicator group for habitat fragmentation, anthropogenic disturbance and climate change effects (Larsen 1993; Heikkinen et al. 2009; Manzoor et al. 2013). Their life cycle highly depends on plants either for breeding (host plants) or food (nectar) and multiple other environmental factors (Collinge et al. 2003; Manzoor et al. 2013). They can serve as indicators for biodiversity in ecological studies due to their sensitivity to even minor changes in habitat conditions or disturbances (Lomov et al. 2006; Bouyer et al. 2007; Dobson 2012). In addition, butterflies play an essential ecological role as pollinators and herbivores (Courtney et al. 1982; Bonebrake et al. 2010; Rader et al. 2015). Herbivory has been valued as a mechanism that has promoted plant co-existence and diversity, while pollination has enhanced plants life, growth and diversity (Vail 1992; Coley and Barone 1996; Viola et al. 2010). Moreover, their association with particular forest types and host plants, the fluctuation in their richness and abundance according to seasonality and their pervasive presence on the territory makes them perfect study subjects for investigating and monitoring the conservation status of ecosystems (Lien 2007; Monastyrskii 2007; Habel et al. 2018). This co-existence and interplay between butterflies and plants offers a unique fundamental contribution to ecosystem functioning while presenting a huge potential in tropical forests biodiversity monitoring (Humpden and Nathan 2010).

Vegetation diversity enhances ecological complexity by increasing the availability of nectar sources, larval host plants and microclimatic niches (Vu et al. 2015). Structural characteristics, such as canopy height, foliage density and vertical stratification, further influence microhabitats and resource accessibility, directly impacting butterfly foraging behaviour, oviposition and survival (Collinge et al. 2003). Consequently, areas with high vegetation heterogeneity are often associated with greater butterfly species richness and more stable community structures.

Despite this well-established relationship, the extent to which vegetation diversity and structure shape butterfly assemblages remains poorly documented in many tropical and subtropical ecosystems. This is more pronounced especially in East Africa, a region known for its ecological heterogeneity and high biodiversity. The Arabuko-Sokoke Forest (ASF) in coastal Kenya presents a unique opportunity to investigate these relationships, as it encompasses a mosaic of distinct forest types within a relatively compact landscape, enabling detailed comparisons of butterfly community assembly across environmental gradients. The forest hosts four butterfly species endemic to the forests of Kenya and Tanzania: *Acraea matuapa*, *Baliochila latimarginata*, *Baliochila stygia* and *Charaxes blanda*, 50 nationally and globally rare plant species, three rare endemic mammals and is home to 230 bird species, 15 of which are rare and endemic to the Kenyan coast (ASF Management Team 2002). The forest also plays a crucial role as a global eco-tourism site, while locally supporting survival of the forest adjacent indigenous people livelihoods who depend on the forest for butterfly farming, collecting medicinal plants and wood production.

Moreover, although ASF is rich in plant diversity and butterfly diversity, little is known about their interaction. Limited butterfly studies carried out in ASF have looked at the butterfly diversity across the forest and forest types or seasonality influence on butterfly diversity (Ayiemba 1995; Habel et al. 2018). However, to our knowledge, there is no study that has thoroughly investigated the influence of the plant species diversity on butterfly diversity in ASF. Moreover, the need to regularly assess and monitor its continued fragmentation and biodiversity is therefore fundamental for long-term conservation efforts (Azeria et al. 2007; MacFarlane et al. 2015; Habel et al. 2017; Busck-Lumholt and Treue 2018). In this study, we investigate the relationships between vegetation structure and butterfly community structure and species diversity within the Arabuko-Sokoke Forest (ASF). This was achieved through systematic sampling along 100-m transects across different forest types, conducted over a four-month period, incorporating a range of butterfly functional traits to enhance ecological interpretation.

In particular, we investigate: (i) how the dominant forest types influence butterfly species diversity, composition and abundance in ASF; (ii) how plant species diversity influence or correlate with butterfly diversity and composition and (iii) how butterfly wingspan traits vary across different forest types. We synthesise these results to better guide the conservation policy formulations for sustainable forest use and management of the forest, especially in the dry season when this study was conducted.

Materials and methods

Study area and forest types

The Arabuko Sokoke Forest (ASF) is the largest forest fragment remaining within the Kenyan coastal forests covering an area of 42,000 ha, the second being Shimba Hills Forest (25,300 ha; Fig. 1A; Burgess and Clarke (2000); Fungomeli et al. (2020a)). It is globally valued as a world biodiversity hotspot of the Eastern Arc and Coastal Forests of Kenya and Tanzania (Myers et al. 2000). ASF is a centre of endemism, hosting a conspicuous number of threatened and endangered species and recently declared a UNESCO Biosphere Reserve (UNESCO 2019). Anthropogenic pressure and biodiversity loss, together with climate change are heavily impacting tropical forests, such as the Arabuko Sokoke Forest in Kenya (Burgess and Clarke 2000; Newton and Echeverría 2014; FAO 2018; Fungomeli et al. 2025).

As a dry lowland coastal forest, ASF spreads between the cities of Kilifi in the south and Malindi in the north, positioned between 39°48'E and 40°00'E longitude and between 3°11'S and 3°29'S latitude (Fanshawe 1995; Muchiri et al. 2001). It lies on a flat coastal plain at sea level and the area is divided by a low escarpment which crosses the forest from south-west to north-east (Moomaw 1960; Fanshawe 1995).

The climate consists of rainy and dry seasons, with two rainfall seasons of long and short rains. The long rainy season occurs from April to July; short rains from October to December, while the dry season lasts from December to March and in August/September (Burgess and Clarke 2000; Omenge 2002). The annual rainfall ranges from 600 to 1,000 mm, with rainfall decreasing from east to west within the Forest (Omenge 2002; Habel et al. 2017). Temperature ranges from monthly averages of 24 °C and 30 °C and humidity is about 60% annually (Burgess and Clarke 2000). Several water pools exist within the Forest during the rainy season with most drying out in the dry season and there are no rivers within the forest (Fungomeli et al. 2001; Kanga 2002; Muriithi and Kenyon 2002).

A defining characteristic of the Arabuko-Sokoke Forest is the presence of distinct vegetation types, usually referred to as forest types (Fig. 1B–E). These forest types are closely associated with the underlying soil characteristics. The area features two predominant soil types: light, white sandy soils and heavier, red clay soils (Fanshawe 1995; Muchiri et al. 2001). These contrasting soil conditions have significantly influenced the distribution and composition of the forest's vegetation communities. The four distinct forest types are the *Cynometra* forest, *Brachystegia* forest, Mixed forest and the forest edge (Fig. 1B–E).

Cynometra **forest**

The *Cynometra* forest, which occupies the western sector of the ASF, is the most extensive of the forest types, accounting for over 50% of the forest area (Fanshawe 1995). This zone is found predominantly on red clay soils and is characteried by a dense, low-statured canopy, composed mainly of *Cynometra*

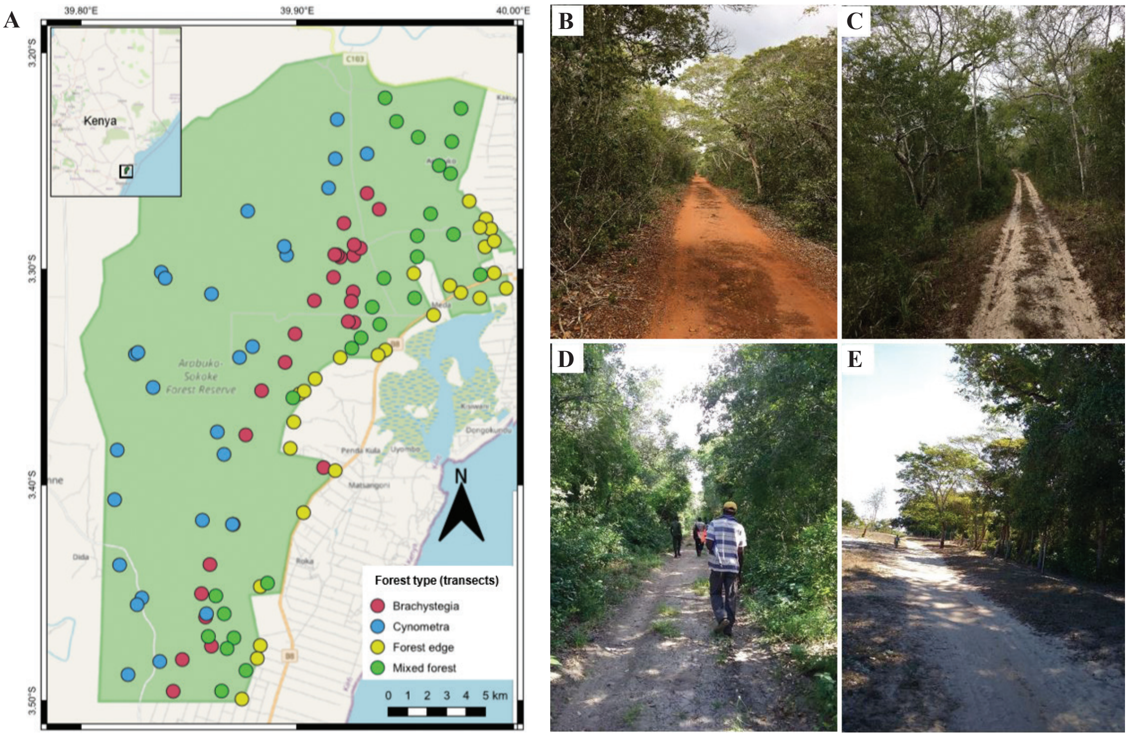

Figure 1. A. Map of Arabuko Sokoke Forest, Kenya, showing the distribution of the 108 studied butterfly transects within the four forest types: *Brachystegia*, *Cynometra*, Mixed forest and Forest edge. **B–E.** The four forest types study sites within Arabuko Sokoke Forest, Kenya showing. **B.** *Cynometra* forest; **C.** *Brachystegia* forest; **D.** Mixed forest; **E.** Forest edge. Photo credits: Maria Fungomeli.

webberi, *Cynometra suhalensis* and *Manilkara sulcata*, with occasional emergents, such as *Euphorbia candelabrum* (Fig. 1). The undergrowth is sparse due to the closed canopy and low light penetration, creating a relatively stable microclimate with reduced temperature fluctuations and high humidity.

***Brachystegia* forest**

Brachystegia forest is located centrally within the ASF, on the nutrient-poor, white sandy soils and covers approximately 18% of the forest (Fig. 1; Muchiri et al. 2001). It is dominated by *Brachystegia spiciformis*, characterised by an open canopy structure interspersed with grasses and shrubs, resulting in a more sunlit and drier environment than other forest types. The floristic composition is adapted to dry conditions and the habitat is important for butterfly species, reptiles and birds that depend on high light availability and open understoreys. Additionally, the openness of this zone creates microhabitats favourable for thermoregulation and basking, crucial for many invertebrate and herpetofauna species.

Mixed forest

The mixed forest type is located in the eastern part of the Forest, where it grows on grey sandy soils that retain more moisture than the white sands, but are lighter than the red clay soils. This forest type represents about 17% of the Reserve and is notable for its high plant species richness and vertical stratification (Fanshawe 1995; Muchiri et al. 2001; Arabuko Sokoke Management Team 2002). It is dominated by mixed plant species of *Afzelia quanzensis*, *Hymenaea verrucosa*, *Newtonia hildebrandtii* and *Manilkara sansibarensis*.

Forest edge

The forest edge was selected along the transition from the mixed forest of the Arabuko-Sokoke Forest (ASF) to adjacent agricultural lands. This ecotone represents a gradual shift from intact forest ecosystems to human-modified landscapes and coastal habitats (Fig. 1; Muchiri et al. 2001). It is characterised by a heterogeneous mosaic of land uses, including subsistence farms, scattered shrubs and open grassy clearings. Structurally, it exhibits increased light penetration, higher temperature fluctuations and reduced canopy cover compared to the forest interior. These conditions create a distinctive microclimate that supports a unique assemblage of flora and fauna adapted to edge environments.

Data collection

Field sampling and data collection were conducted during the dry season months (January-April) of 2019 across the four forest types of ASF: *Cynometra* forest, *Brachystegia* woodland, mixed forest and forest edge (Fig. 1). Butterflies were sampled by using a standard number of 27 transects within each vegetation type leading to a total of 108 transects. Each transect measured 10 m × 100 m. Butterflies were recorded in each transect by using a standard count technique performed by walking at slow constant pace for approximately 15 min. All butterfly species seen on both sides of the path were recorded. Each transect was surveyed once per day, every day, throughout the four-month dry season (January-April 2019), ensuring comprehensive and exhaustive species detection in accordance with established butterfly monitoring protocols (Pollard 1977; Pollard and Yates 1993).

Butterflies were identified and recorded at species level. Specimens that could not immediately be identified in the field were caught with a butterfly net and placed in numbered envelopes or photographed for further identification in the lab. Identification was carried out using the butterfly references for the area (Larsen 1991) and supported by taxonomic counter checks from published sources. All transects were geo-referenced, with details of date, hour of start and end.

Vegetation field sampling was performed by using 27 plots each measuring 10 m × 100 m (same used for butterfly transects hereafter referred to as plots) and internally subdivided into 20 subplots of 10 m × 5 m. Each vegetation plot corresponded to a butterfly transect. Within the plots and subplots, we identified and measured the height and diameter at breast height (DBH) for each individual woody plant species (trees, lianas and shrub) with DBH ≥ 5 cm. Plants with DBH < 5 cm, such as small shrubs, were identified in two subplots of each plot (see Fungomeli et al. 2020a, 2020b).

Butterfly traits: wingspan sizes

We compiled and obtained wingspan sizes for our sampled butterfly species from published data sources of Woodhall (2005), Woodhall (2020), Schmitt (*pers. comm*), Barcode of Life Data System database (https://v3.boldsystems.org) and from the collection of the Senckenberg German Entomological Institute, Müncheberg.

All butterflies encountered along the transects were classified according to their ecological traits and distribution. The larval diet of each species was determined, based on host plant use and categorised into one of three trophic breadth classes: (1) monophagous, restricted to a single host plant genus; (2) oligophagous, restricted to host plants within a single plant family; or (3) polyphagous, utilising host plants from multiple plant families. A further classification into endemic status was assigned to species according to Larsen (1996).

Data analysis

A community matrix was prepared for the butterfly species abundances and another matrix was prepared for the woody plant species across the forest types.

Butterfly species diversity

Butterfly species diversity was analysed in terms of species richness, Shannon index and Simpson index across forest types:

$$\text{Shannon Index:} \quad H = \sum_{i=1}^{k} p_1 \ln(p_1)$$

$$\text{Simpson Index:} \quad D = 1 - \sum_{i=1}^{k} p_1^2$$

For both indices, k represents the total number of species, while p_i indicates the relative abundance of each species that is calculated as n_i/N (in which n_i indicates the number of individuals of the i-species and N indicates the number of individuals of all species within the transect.

Butterfly species richness and mean abundance distributions across forest types were visualised using boxplots. Mann-Whitney U test for pairwise comparisons was used to compare species richness and abundance amongst forest types. Additionally, rank-abundance curves were constructed for each forest type to illustrate patterns of species dominance and evenness (Whittaker 1965).

Rarefaction curves and species diversity estimation

To assess and compare species diversity across forest types, we employed sample coverage-based rarefaction and extrapolation within the Hill numbers framework (Chao et al. 2014). We analysed abundance data for each forest type using the iNEXT() function from the iNEXT package in R (Hsieh et al. 2016), specifying datatype = "abundance". This function performs both interpolation (rarefaction) and extrapolation of diversity estimates, based on individual-based abundance data. Confidence intervals (95%) were derived using 1,000 bootstrap replicates. Following Chao et al. (2014), extrapolation was constrained to a maximum of twice the reference sample size to maintain estimate stability.

Correlation between butterfly and plant species diversity

We applied a symmetric Co-correspondence analysis (CoCA) to quantify relationships between the plant species community with the butterfly species community across the forest types. Co-correspondence analysis is useful for comparing biological communities where observations have been made at the same locations (Braak and Schaffers 2004). We did this by a weighted average of species abundance values for plant species and separately for butterfly species within each of the forest types. We used '*coca'* function of the 'cocorresp' R package (Simpson 2009) to correlate the butterfly and plant communities using the 'symmetric' method. All graph plotting was performed using R package *ggplot2* (Wickham 2016) and *ggrepel* (Slowikowski 2020).

Butterfly species composition

We square-root transformed butterfly community abundances prior to the analysis to reduce effects of dominant species. Transformed community abundances were then used to generate a Bray-Curtis dissimilarity matrix (Bray and Curtis 1957). We tested for species composition differences in the butterfly community structure amongst forest types by an analysis of similarities (ANOSIM) using the '*anosim'* function of the 'vegan' R package (Oksanen et al. 2020). We also tested for significant differences between forest types using the permutational analysis of variance (PERMANOVA), using the '*adonis'* function of the 'vegan' R package. All tests were conducted using 999 permutations. Butterfly species contributing to similarities across forest types were determined using similarity percentages analysis (SIMPER). *P*-values were adjusted using the Benjamini-Hochberg test to control the false discovery rate. This approach was selected for its ability to limit type I errors, while retaining greater statistical power than more conservative methods, such as the Bonferroni correction.

Beta diversity partitioning

To assess whether variability in butterfly community composition differed amongst the four forest types (*Brachystegia*, *Cynometra*, mixed forest and forest edge), we performed a permutation test for homogeneity of multivariate dispersions (PERMDISP), based on Bray-Curtis dissimilarities using the '*betadisper'* function in the *vegan* R package. We then evaluated beta diversity amongst the four forest types. We quantified multi-site beta diversity using the abundance-based extension of the '*betapart'* framework (Baselga et al. 2017), implemented via the '*beta.multi.abund'* function in the R package betapart (v. 1.6). This method partitions Bray-Curtis dissimilarity into three components: (i) total beta diversity (β_total); (ii) balanced variation in abundance (β_balanced) and (iii) abundance gradients (β_gradient).

We also assessed spatial heterogeneity of community composition within forest types by testing homogeneity of multivariate dispersion. Bray-Curtis dissimilarities, calculated from species abundance data, were used to compute distances of individual plots to their respective group centroids using the '*betadisper'* function in the R package vegan (Oksanen et al. 2020). These distances reflect within-group variation in community composition. Differences in dispersion amongst forest types were tested using ANOVA, followed by Tukey's Honest Significant Difference (HSD) post-hoc tests.

Butterfly composition – NMDS

To visualise differences in butterfly species composition amongst forest types, we conducted a non-metric multidimensional scaling (NMDS) analysis, based on Bray-Curtis dissimilarities (Kruskal 1964). Prior to analysis, butterfly species abundance data were square-root transformed to reduce the influence of highly abundant species. NMDS was performed using the '*metaMDS'* function from the *vegan* package (Oksanen et al. 2020) in R (R Core Team 2020). This function conducts automatic data standardisation, multiple random starts and iteration to ensure a stable and optimal ordination solution. Groupings by forest type were visualised using convex hulls.

Butterfly traits: wingspan sizes

Using Pearson correlation, we correlated butterfly wingspan sizes across forest types, by first correlating for total abundances in all forest types and then second within each vegetation type. Following confirmation of normality, pairwise t-tests were conducted to compare average wingspan sizes across different forest types. To account for multiple comparisons and control the false discovery rate, p-values were adjusted using the Benjamin-Hochberg test.

Results

We recorded a total of 6,050 butterfly individuals belonging to 86 species, 38 genera and five families across the four forest types of Arabuko Sokoke Forest (Appendix 1). The plant species survey resulted in a total of 178 plant species belonging to 78 genera and 34 families.

Butterfly species diversity

Butterfly species diversity was primarily dominated by the Nymphalidae family, which had the highest number of species, followed by Pieridae, Papilionidae, Lycaenidae and Hesperiidae (Appendix 1). Analysis on the most abundant butterfly species revealed *Phalanta phalantha*, *Appias epaphia*, *Catopsilia florella*, *Hypolimnas misippus* and *Coeliades forestan*, as the most frequent across all forest types (Suppl. material 1: fig. S1). A strong positive correlation was observed between species richness and abundance across the forest types ($R^2 = 0.89$). The distribution of butterfly larval feeding habits showed oligophagous and polyphagous species being dominant in all forest types (Suppl. material 1: fig. S2).

Rarefaction curves and species diversity estimation

Rarefaction curves revealed the mixed forest exhibited the highest species richness, followed by *Brachystegia* forest, forest edge and *Cynometra* forests (Fig. 2). Rarefaction curves for all forest types approached asymptotes, indicating sufficient sampling and species richness capture, except in the *Brachystegia* forest, where the non-asymptotic curve suggests that further sampling may uncover additional species.

Table 1. The butterfly species diversity across forest types, showing cumulative species richness and abundance, Shannon index and Simpson index per vegetation type in Arabuko Sokoke Forest, Kenya.

Species diversity	*Brachystegia*	*Cynometra*	Forest edge	Mixed forest
Cumulative species richness	50	40	52	80
Cumulative species abundance	1022	1112	2141	1775
Shannon's H Index	2.38	2.58	2.87	2.66
Simpson's 1-D Index	0.9	0.9	0.93	0.91

Butterfly species richness and abundances across forest types showed that the mixed forest had the highest cumulative species richness, followed by *Brachystegia* and forest edge, while *Cynometra* had the lowest value (Table 1). Average species richness and abundance per plot varied across forest types, with significantly higher abundance values observed at the forest edge and in mixed forest habitats (ANOVA, $P < 0.05$; Fig. 3). According to ANOVA, differences amongst species richness per transect were at the significance threshold amongst forest types ($P = 0.05$), while species abundances per transect were significantly different ($P = 0.001$; Fig. 3). Pairwise comparisons of butterfly abundance revealed significant differences between *Cynometra* forest and forest edge ($P = 0.001$), *Brachystegia* forest and forest edge ($P = 0.013$), as well as between *Brachystegia* forest and forest edge ($P = 0.001$; Fig. 3).

The diversity indices indicated relatively similar levels of butterfly diversity across vegetation types. Shannon index values ranged from 2.91 ± 0.40 at the forest edge to 2.82 ± 0.42 in the mixed forest, while the Simpson index values ranged from 0.93 ± 0.04 to 0.92 ± 0.03.

Beta diversity partitioning

Multivariate dispersions revealed significant difference in multivariate dispersion across the four forest types (F = 3.893, $P = 0.007$). Therefore, variation in butterfly community composition may in part be influenced by differences in within-forest type heterogeneity. Multi-forest type beta diversity analysis (β) revealed consistently high total dissimilarity across forest types, with β_total values ranging from 0.885 to

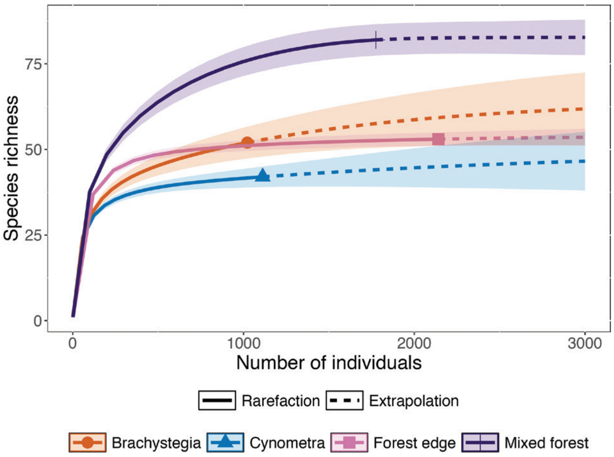

Figure 2. Rarefaction curves showing species richness as a function of number of individuals across the sampled forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in the Arabuko Sokoke forest, Kenya. Each solid line represents actual sampled species (interpolated), and the dashed-line represents extrapolated individuals (extrapolated). Shaded areas represent 95% confidence interval.

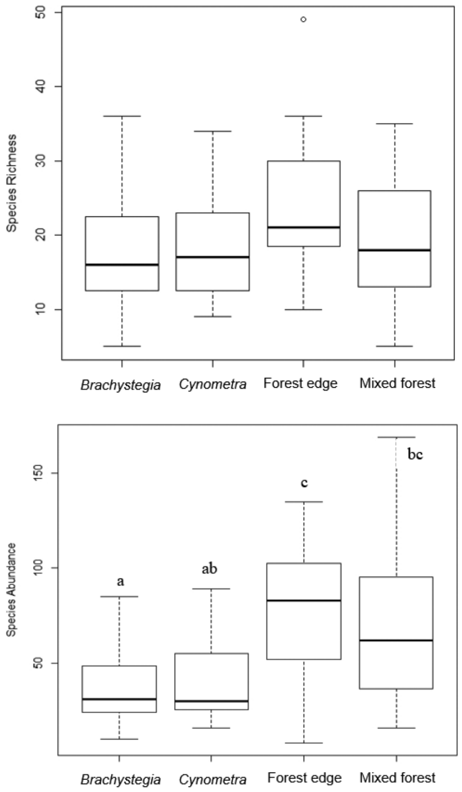

Figure 3. Boxplots showing butterfly species richness and abundances comparison across the four forest types of *Brachystegia*, *Cynometra*, Forest edge and Mixed forest in the Arabuko Sokoke Forest, Kenya. Forest type with different letter denotes statistical significant differences ($P < 0.01$).

0.910 (Table 2). The largest contribution to beta diversity came from balanced variation in species abundance (β_balanced: 0.803–0.837), indicating that community compositional differences were primarily driven by species turnover in abundance rather than nestedness (β_gradient: 0.067–0.096) (Table 2). *Brachystegia* forest exhibited the highest total beta diversity (β_total = 0.910), suggesting substantial heterogeneity in community composition across plots. Forest edge had the lowest β_total (0.885), while *Cynometra* and Mixed forests showed intermediate values (Table 2).

Spatial dispersion of community composition

Spatial heterogeneity within forest types, assessed via multivariate dispersion, varied significantly (Table 2). *Brachystegia* forest exhibited the highest dispersion (mean distance = 0.45), indicating greater spatial variability in species composition. These results reflect substantial spatial heterogeneity in species abundances in *Brachystegia*. In contrast, forest edge had the lowest dispersion (median ~ 0.33), indicating more homogeneous community structure. Tukey HSD tests confirmed dispersion in *Brachystegia* was significantly greater than at forest edges ($P = 0.006$), while other pairwise comparisons were not statistically significant (Table 2). These results reflect that forest edge communities are more similar to each other, while *Brachystegia* forest is more ecologically diverse. Overall, beta diversity results indicate that abundance-based species turnover drives community differentiation across forest types, with *Brachystegia* forests supporting more spatially heterogeneous communities, while forest edges harbour more homogenised assemblages.

Correlation between butterfly and plant species diversity

Co-correspondence analysis (CoCA) revealed a strong correlation between the species composition of plants and butterflies across the forest types. The correlation coefficients for Axis 1 and Axis 2 between the butterfly and plant communities were 0.991 and 0.994, respectively. The eigenvalues for the first and second axes indicated the contribution of each axis to the total inertia, with values of 0.022 and 0.012, representing a variance of 57.3% and 32.6%, respectively. This resulted in a total explained variance of 89.9% (Fig. 4), highlighting a robust and highly significant correlation between the community matrices of plants and butterflies.

Butterfly species composition

The NMDS analysis of butterfly species composition across forest types revealed considerable overlap, with no clear separation observed amongst the different forest types, with *Cynometra* forest covering a wider NMDS space that overlaps *Brachystegia*, forest edge and mixed forest (Fig. 5, Table 2). Butterfly assemblages across different forest types showed substantial overlap, with many species occurring in more than one forest type within the ASF. A pairwise permutational multivariate analysis of variance (PERMANOVA) revealed statistically significant compositional differences in butterfly assem-

Table 2. Summary of beta diversity metrics across the four forest types, including abundance-based partitioning components of total beta diversity (β_total); balanced variation (β_balanced); and abundance gradient (β_gradient), as well as multivariate dispersion (measured by the mean distance to centroid. Tukey HSD post hoc tests were used for pairwise comparisons amongst forest types (n.s. = no significant difference).

Forest type	n(plots)	β_total	β_balanced	β_gradient	Mean dispersion (distance to centroid)	Significant difference (Tukey HSD)
Brachystegia	27	0.910	0.825	0.085	0.452	higher than forest edge ($P = 0.006$)
Cynometra	27	0.903	0.837	0.067	0.425	n.s. vs. other types
Mixed forest	27	0.903	0.807	0.096	0.418	n.s. vs. other types
Forest edge	27	0.885	0.803	0.083	0.364	Lower than *Brachystegia* ($P = 0.006$)

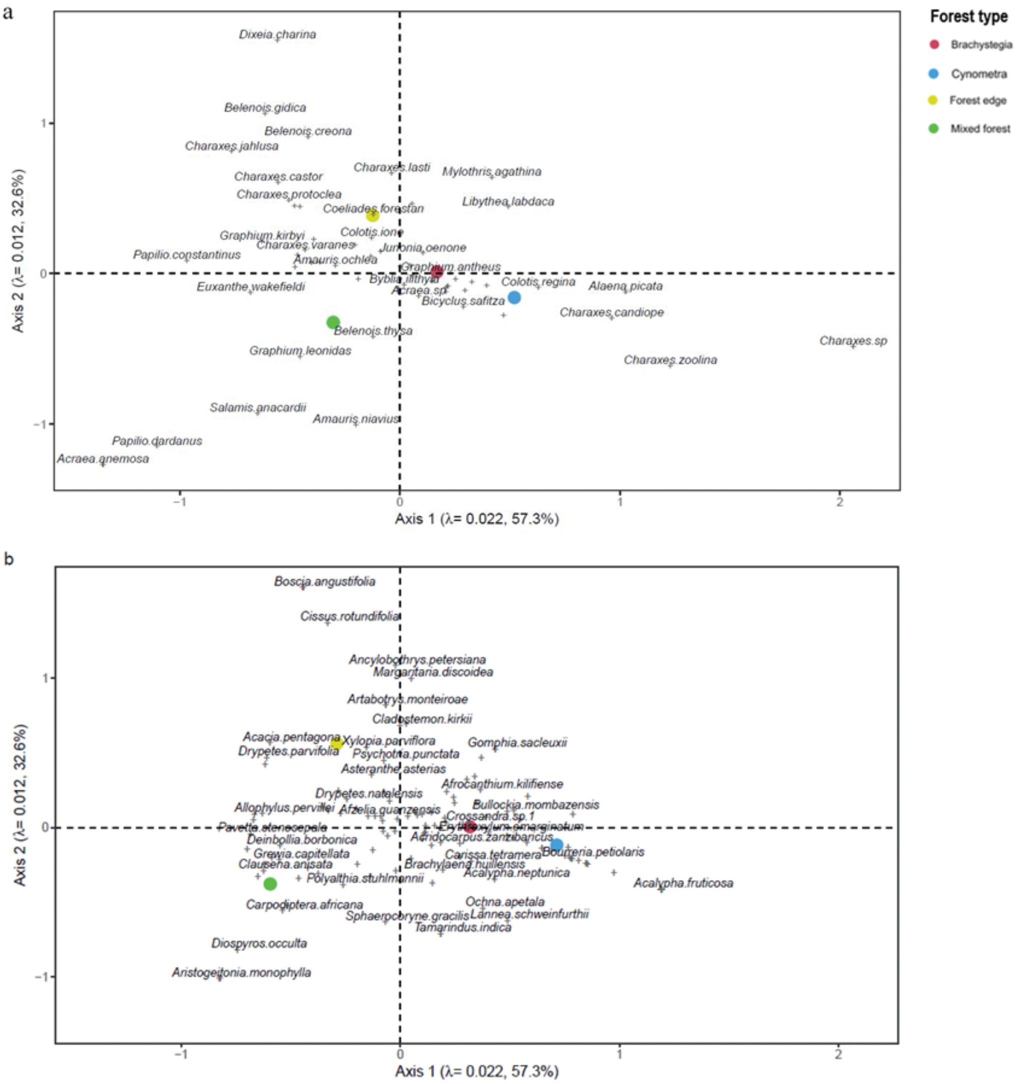

Figure 4. Symmetric co-correspondence analysis (CoCA) ordination bi-plots showing correlations between (**a**) butterfly and plant species and (**b**) plant and butterfly species within the four forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in Arabuko Sokoke Forest, Kenya. The Axis-1 eigen value of 0.022 explains a variance of 57.3% and Axis-2 eigen value of 0.012 explains a variance of 32.6%. Total explained variance by Axis 1 and 2 is 89.9%.

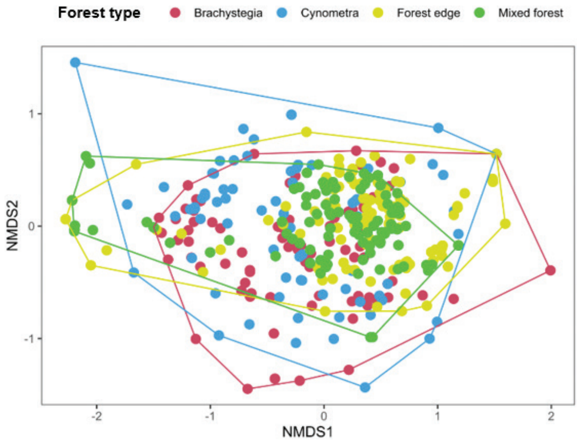

Figure 5. Non-metric multidimensional scaling (NMDS) for butterfly species composition within the four forest types of Arabuko Sokoke Forest, Kenya. Different colours represent different forest types as follows: *Brachystegia* (red), *Cynometra* (blue), Mixed forest (green), Forest edge (yellow).

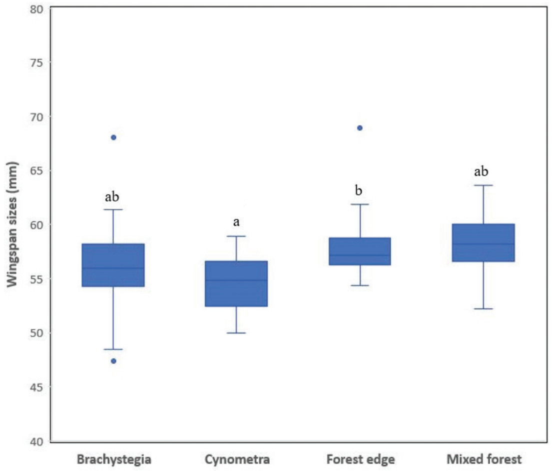

Figure 6. Butterfly average wingspan sizes across the four forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in Arabuko Sokoke Forest. Forest type with different denotes significant difference ($P < 0.01$).

blages amongst the forest types ($R^2 = 0.07$; $P = 0.006$). Additionally, SIMPER results show species composition differences amongst forest types that contribute up to 70% of the observed dissimilarities (Appendix 2).

Butterfly traits: wingspan sizes

Average wingspan sizes were significantly larger at the forest edge compared to the *Cynometra* forest ($P < 0.01$; Fig. 6). However, no significant correlation was found between wingspan size and species abundance across forest types (Fig. 7).

Butterfly traits: larval feeding habits

The majority of larvae from the species encountered were classified as oligophagous, followed by polyphagous species and a smaller number classified as monophagous (Suppl. material 1: fig. S2). Overall, Oligophagous species constituted the largest share of individuals across all forest types, accounting for 63.4% of butterflies at the forest edge and reaching up to 67.5% in the mixed forest (Suppl. material 1: fig. S2).

Discussion

This study investigated the influence of vegetation diversity and structural complexity on butterfly community composition and species richness within Arabuko Sokoke Forest (ASF), a coastal biodiversity hotspot in East Africa. Our results provide new insights into butterfly community composition across habitat types within the Arabuko Sokoke Forest and their associations with plant communities. By examining species distributions alongside vegetation data, we highlight both broad and fine-scale patterns relevant to biodiversity conservation in tropical forest mosaics.

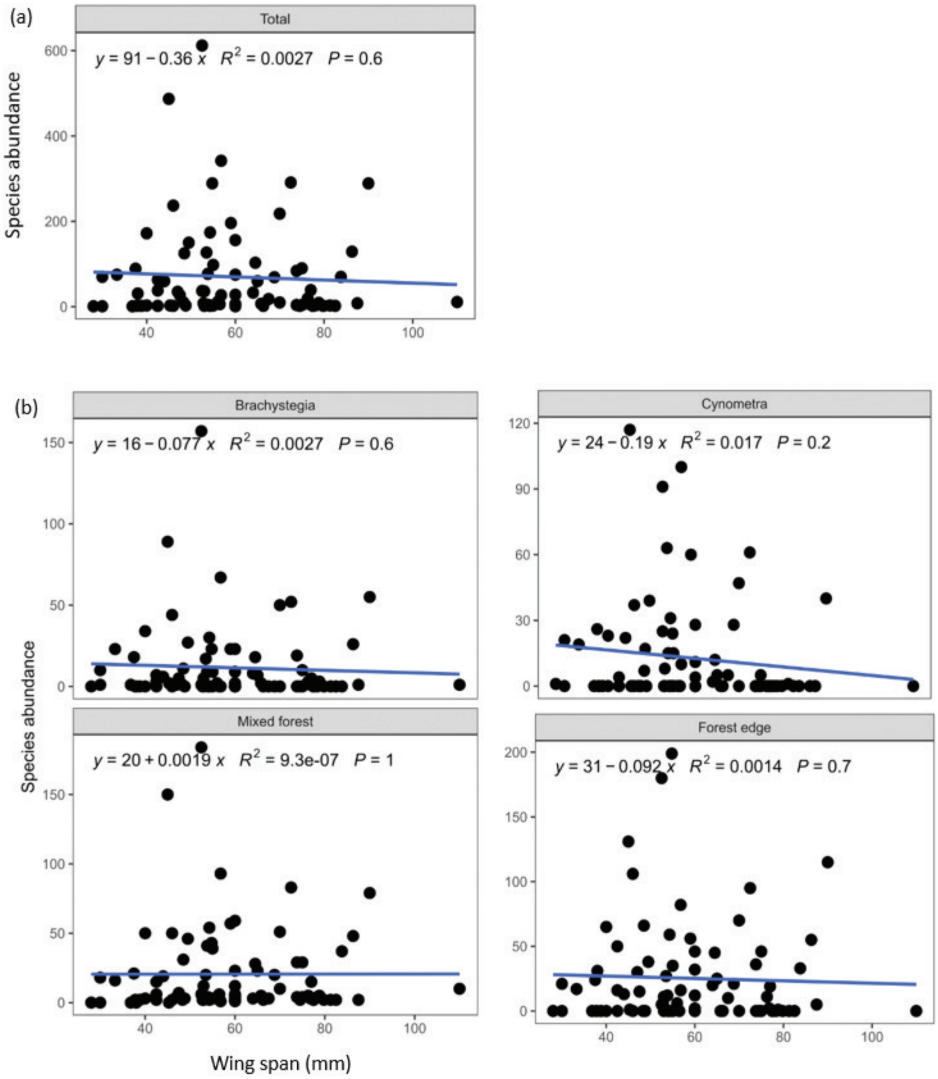

Figure 7. Butterfly wingspan sizes correlation across the four forest types of Arabuko Sokoke Forest, Kenya. Showing wingspan correlation for (**a**) The total correlation in the four forest types (**b**) the correlation for each forest type of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge.

Butterfly community structure and habitat overlap

Butterfly assemblages across different forest types showed substantial overlap, with many species occurring in more than one forest type within the Arabuko Sokoke Forest. This pattern of overlap suggests a degree of functional connectivity between habitats, where butterflies may move freely across forest types for resource availability, to access nectar sources, host plants or suitable microclimates for thermoregulation and breeding (Aguirre-Gutiérrez et al. 2017). Such overlap is ecologically significant, as it implies that, while habitat types may differ in structure and floristic composition, they are not functioning as isolated ecological units for butterflies. Rather, these habitats may form a complementary mosaic that supports butterfly movement and persistence. This could be particularly important in fragmented landscapes, where connectivity between habitat patches is critical for maintaining viable populations.

As our study was limited to a single dry season, we acknowledge that seasonal variation could play a significant role in shaping butterfly community structure in ways that our data do not currently capture. A study by Habel et al. (2018) in ASF found that butterfly communities showed reduced community overlap amongst habitats during the rainy season. This discrepancy may reflect seasonal shifts in resource availability and changed microclimatic conditions. For instance, increased vegetation growth during the wet season may alter habitat structure, increase flowering plants and fruits for both nectar and fruit feeders and accessibility of host plants, leading to more specialised or stratified butterfly distributions (Castor and Espinosa 2015). In addition, species with narrower ecological requirements might emerge or become more dominant during the rainy season, thereby reducing the community-level overlap. Long-term or seasonally repeated surveys would be essential to determine how stable these patterns are over time and to what extent butterfly habitat associations fluctuate in response to environmental seasonality. Incorporating a temporal dimension into future studies could also help disentangle the relative importance of spatial versus seasonal drivers of diversity and overlap in tropical butterfly communities.

Relationship between plant and butterfly patterns

Our findings revealed a strong positive correlation between plant community composition and both butterfly diversity and assemblage structure across distinct forest types. This underscores the critical role of floristic diversity and vegetation architecture in shaping insect communities and confirms a fundamental ecological relationship between butterflies and the plants that comprise their habitats (Larsen 1991). This finding points to the foundational role that vegetation plays in structuring butterfly communities. Given that butterflies are closely tied to their host plants for larval development and to nectar-bearing and fruiting plants for adult foraging, this floristic diversity strongly predicts butterfly richness and composition. Importantly, what is the strength and clarity of this correlation within a relatively small spatial scale and across naturally occurring forest types within ASF is noteworthy. Such robust cross-taxa associations are rarely reported in ecological studies conducted in the Tropics, where insect diversity often responds to a complex interplay of biotic and abiotic factors (Checa et al. 2014). In many systems, insect-plant relationships are masked by noise from microclimatic variability, dispersal dynamics or seasonal shifts (Checa et al. 2014). Our results, however, suggest that in Arabuko Sokoke, vegetation composition acts as a strong and consistent environmental filter, shaping butterfly assemblages in a predictable way. This reinforces the importance of plant diversity not only as a foundation for ecosystem structure, but also as a practical proxy for broader biodiversity patterns with significant implications for conservation planning and biodiversity monitoring.

Butterfly diversity patterns

Butterfly species richness and abundance varied notably across forest types. The mixed forest exhibited the highest cumulative species richness, followed by the forest edge and *Brachystegia* forest, while *Cynometra* forest supported the lowest species richness and abundance. Butterflies, as herbivorous insects, often exhibit narrow larval host plant specificity and selective adult nectar preferences, making them highly responsive to changes in plant community composition. This strong trophic linkage means that variation in plant diversity and abundance directly affects butterfly community structure. As previously observed by Larsen (1991), different butterfly species display distinct preferences for larval host and less for nectar plants, particularly during breeding and foraging periods. In ASF, the high plant species richness likely supports a broad range of butterfly guilds, contributing to the overall high butterfly diversity observed in the region. Moreover, our findings are consistent with broader ecological theory, which hypothesise that plant-insect interactions are mediated not only through direct resource relationships, but also via indirect mechanisms, such as vegetation structure and associated microclimatic conditions (Steffan-Dewenter and Tscharntke 1997; Aguirre-Gutiérrez et al. 2017; Oliveira et al. 2021). Thus, structurally diverse vegetation can buffer environmental extremes and provide varied microhabitats, enhancing survivability and niche partitioning amongst butterfly species.

The significance of these findings is particularly notable in the East African context, where community-level studies examining cross-trophic linkages remain limited. The novelty of this study lies not only in the strength of the observed plant-butterfly correlation, but also in the implication that butterfly assemblages could serve as sensitive bioindicators of plant community composition and forest integrity. Given their rapid response to habitat changes, butterflies offer a valuable, cost-effective means for monitoring ecological health, particularly in data-deficient tropical regions, such as ASF. In light of increasing anthropogenic pressures on East African forest ecosystems, including habitat fragmentation, selective logging and land-use conversion, our results emphasise the need to conserve floristically rich and structurally complex vegetation to maintain both plant and insect biodiversity. Integrating butterfly monitoring into conservation planning could enhance early detection of ecosystem degradation and provide information for adaptive management strategies.

The role of forest types

This study highlights differences in butterfly community structure across forest types, emphasising the distinct ecological contributions of each habitat to local and landscape-scale diversity. Butterfly abundance varied significantly amongst the different forest types, while species richness did not show significant difference. Beta diversity analyses revealed consistently high community dissimilarity across all forest types, driven predominantly by balanced variation in species abundances rather than nestedness. Consequently, species turnover, rather than richness differences, is the primary mechanism structuring butterfly communities at the landscape scale in ASF. Notably, the highest species abundance was recorded at the forest edge; however, they also exhibited reduced species turnover and lower community dispersion. The mixed forest supported the highest cumulative species richness, while *Brachystegia* forests, despite lower local species richness and abundance, contributed most to beta diversity and spatial heterogeneity. The high species turnover observed suggests that *Brachystegia* forest maintains a diverse and spatially variable butterfly community, potentially driven by microhabitat differences or floristic specialisation (Legendre et al. 2005). Overall, abundance-based species turnover is a key driver of butterfly community differentiation across forest types, highlighting the conservation value of structurally complex and spatially heterogeneous habitats like *Brachystegia* forest.

High species abundance at the forest edge can be explained by the possible presence of microhabitat niches of biotic and abiotic resources that support the availability of food and flowering plants for nectar feeding, especially during the dry season when most forest vegetation is not flowering. This pattern is largely attributed to the ecological blending of habitat types at forest edges, where forest edges often support both forest-dependent species and species adapted to open or semi-open environments. In addition, forest edges are typically associated with increased levels of disturbance, including greater exposure to light, wind and human activity, which can significantly alter habitat structure and microclimatic conditions (Habel et al. 2025). In ASF, this trend is evident across the forest types surveyed. Forest-interior specialists, such as *Euxanthe wakefieldi*, *Amauris niavius* and *Amauris ochlea*, were predominantly observed within the mixed forest interior, where micro-climatic stability and specialised host plants are more likely to be present. In contrast, habitat generalists like *Hypolimnas misippus*, *Phalanta phalantha* and *Catopsilia florella*, which tolerate a wider range of ecological niches and host plants, were more frequently recorded at forest edges. As a result, overall species abundance may be elevated in edge habitats, not due to the presence of rare or conservation-priority taxa, but because of the additional contribution of widespread, disturbance-tolerant generalists (Blair and Launer 1997; Bobo et al. 2006).

Moreover, forest edges host a synergy of cultivation around the forest edge, where agricultural activities promote herbaceous species that cannot be found in the forest during the dry season (Habel et al. 2025). These herbaceous plants provide a variety of flowers for butterflies to feed on during the dry season (Bonebrake et al. 2010). This characteristic makes the forest edge a place mainly devoted to feeding, while other vegetation habitats may be preferred for reproduction and oviposition. Consequently, relying solely on species richness or overall diversity as a metric for conservation planning can be misleading. High diversity in edge or disturbed habitats may mask the loss or decline of forest specialists, whose presence is a more accurate indicator of ecological integrity and long-term ecosystem health. Thus, assessing conservation value requires a species-specific approach that prioritises the occurrence, abundance and habitat fidelity of specialist taxa, particularly those confined to forest interiors.

In addition, the mixed forest within ASF appears to maintain relatively moist and stable microclimatic conditions, owing to its tall canopy cover, sub-canopy layers, variable understorey and favourable soil characteristics (Fanshawe 1995; Muchiri et al. 2001). These environmental conditions create a wide range of ecological niches which supports several shade-dependent species, including forest-dependent butterflies, likely contributing to its ability to support a higher diversity of butterfly species. Notably, *Papilio dardanus*, a species typically more abundant during the rainy season, was recorded exclusively in the mixed and *Brachystegia* forest types during this survey, i.e. during the dry season. This unusual seasonal presence suggests that the mixed forest offers sufficiently favourable microhabitats to buffer against seasonal fluctuations in temperature and humidity. A seasonality study by Habel et al. (2018) reported higher butterfly species richness in ASF during the rainy season, highlighting the influence of seasonal conditions, particularly rainfall on butterfly richness. Supporting the occurrence of *P. dardanus*, the plant survey revealed a high abundance of its known host plants, particularly *Clausena anisata*, *Vepris amaniensis* and *Vepris trichocarpa*, within the mixed forest (Fungomeli et al. 2020a, 2020b). The availability of these larval host plants, combined with shaded, humid microclimates, likely creates optimal conditions for the survival and reproduction of *P. dardanus*.

Furthermore, the mixed forest is a preferred habitat for elephants, likely due to its food resources and canopy shade (Habel et al. 2025). Elephant activity contributes indirectly to butterfly persistence: their dung is a critical source of salts and minerals, especially during the dry season and is frequently used by butterflies for nutrient supplementation (Larsen 1996; see also Suppl. material 1: fig. S3). These combined factors, host plant abundance, favourable microclimate and access to nutrient-rich resources, help explain the relatively stable and diverse butterfly assemblages observed in the mixed forest. Given its structural complexity, ecological stability and richness of butterfly species, the mixed forest can be regarded as a key biodiversity 'hotspot' within ASF. Its conservation is therefore of particular importance, especially for sustaining specialist species and buffering biodiversity against climatic and anthropogenic pressures.

Butterfly wingspan sizes across forest types

Butterfly wingspan sizes across forest types were significantly different at the forest edge compared to *Cynometra* forest. This can be attributed to the open-canopy state of the forest edge compared to the closed and dense forest type of the *Cynometra* forest (Hill et al. 2001). Concordantly, butterflies with larger wing sizes can be more abundant in forest gaps which exhibit a wide flight area favouring large-size butterflies. This argument supports our results and explains the high abundance of larger wing-size butterfly at the forest edge (Hill et al. 2001).

Oligophagous species constituted the largest share of individuals across all forest types, accounting for 67.5% of butterflies at the forest edge and reaching up to 63.4% in the mixed forest. The higher relative abundance of oligophagous butterfly species at the forest edge likely reflects the favourable ecological conditions typical of ecotonal environments. Oligophagous species, whose larvae feed on a restricted range of host plants, usually within a single plant family or a few related genera, combine a degree of specialisation with moderate flexibility in host use. This feeding strategy allows them to exploit the structurally and floristically diverse vegetation that characterises forest edges. Such areas generally support a greater diversity and density of sun-loving host plants and nectar resources compared to the shaded interior of *Brachystegia* and *Cynometra* forests. Similar patterns have been reported in other tropical forest systems, where edge habitats harbour a higher abundance of moderately specialised butterflies due to increased resource heterogeneity and microclimatic variation (Bonebrake et al. 2010).

Conclusion and conservation implication

This study underscores the importance of preserving diverse forest types to conserve both local and regional butterfly diversity. While mixed forest enhances richness and abundance, *Brachystegia* forest contributes disproportionately to beta diversity, emphasising their value in maintaining broader ecological variability. Protecting habitat heterogeneity across the landscape is therefore essential to sustaining butterfly diversity and ecosystem function. This study also highlights the strong positive relationship between vegetation composition and butterfly diversity across different forest types within ASF. Our findings demonstrate that vegetation structure and microclimatic conditions play a pivotal role in shaping butterfly community composition.

Notably, the higher butterfly abundance observed at the forest edge reflects the predominance of ecologically flexible, generalist species rather than greater habitat quality, while the mixed forest functions as a reservoir of host plants for breeding. Nonetheless, while forest edges showed elevated species abundance, this was largely due to the presence of generalist species and did not necessarily reflect high conservation value of specialist butterflies. These results underscore the limitations of using species richness alone as a conservation metric and emphasise the importance of beta diversity and species-specific assessments in evaluating habitat quality. These findings also reinforce the potential use of butterflies as ecological indicators for forest integrity and plant community health.

Given increasing anthropogenic pressures and habitat fragmentation in coastal East Africa, conserving structurally complex and floristically rich forest habitats, like those in ASF, is essential. Such efforts are vital not only for maintaining butterfly diversity, but also for preserving broader ecosystem functionality and resilience. In addition, ASF is known for its butterfly farming activities, conducted by communities adjacent to the forest for conservation and educational purposes. Our results provide valuable insights into the relationship between butterfly diversity and forest types. This will help guide the responsible utilisation and conservation of ASF's resources, while preserving its ecological integrity.

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Appendix 1

Butterfly species names with author names, genus and family across the forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in Arabuko Sokoke Forest, Kenya.

Table A1. Butterfly species names with author names, genus and family across the forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in the Arabuko Sokoke Forest, Kenya.

Species	Family
Acraea anemosa Hewitson, 1865	Nymphalidae
Acraea natalica Boisduval, 1847	Nymphalidae
Acraea rabbaiae Ward, 1873	Nymphalidae
Acraea sp.	Nymphalidae
Acraea zonata Hewitson, 1877	Nymphalidae
Alaena picata Sharpe, 1896	Lycaenidae
Amauris niavius Linnaeus, 1758	Nymphalidae
Amauris ochlea Boisduval, 1847	Nymphalidae
Appias epaphia (Cramer, 1779)	Pieridae
Appias lasti Grose-Smith 1889	Pieridae
Bebearia chriemhilda (Staudinger, 1896)	Nymphalidae
Belenois aurota (Fabricius, 1793)	Pieridae
Belenois creona (Cramer, 1776)	Pieridae
Belenois gidica (Godart, 1819)	Pieridae
Belenois thysa (Hopffer, 1855)	Pieridae
Bicyclus safitza (Westwood, 1850)	Nymphalidae
Byblia ilithyia Drury, 1773	Nymphalidae
Catopsilia florella (Fabricius, 1775)	Pieridae
Charaxes bohemani Felder & Felder, 1859	Nymphalidae
Charaxes brutus Cramer, 1779/80	Nymphalidae
Charaxes candiope Godart, 1824	Nymphalidae
Charaxes castor Cramer, 1775/76	Nymphalidae
Charaxes cithaeron Felder, 1859	Nymphalidae
Charaxes etesipe tavetensis Rothschild, 1894	Nymphalidae
Charaxes guderiana Dewits, 1879	Nymphalidae

Species	Family
Charaxes jahlusa Trimen, 1862	Nymphalidae
Charaxes jasius saturnus Butler, 1866	Nymphalidae
Charaxes lasti Grose-Smith, 1889	Nymphalidae
Charaxes protoclea Feisthamel, 1850	Nymphalidae
Charaxes sp.	Nymphalidae
Charaxes varanes (Cramer, 1764)	Nymphalidae
Charaxes violetta Grose-Smith, 1885	Nymphalidae
Charaxes zoolina Westwood, 1850	Nymphalidae
Coeliades forestan Stoll, 1782	Hesperiidae
Colotis amata (Fabricius, 1775)	Pieridae
Colotis auxo (Lucas, 1852)	Pieridae
Colotis danae (Fabricius, 1775)	Pieridae
Colotis eris (Klug, 1829)	Pieridae
Colotis euippe (Linnaeus, 1758)	Pieridae
Colotis ione (Godart, 1819)	Pieridae
Colotis protomedia (Klug, 1829)	Pieridae
Colotis regina (Trimen, 1863)	Pieridae
Colotis vesta (Reiche, 1850)	Pieridae
Cupidopsis iobates (Hopffer, 1855)	Lycaenidae
Danaus chrysippus dorippus Klug, 1845	Nymphalidae
Dixeia charina (Boisduval, 1836)	Pieridae
Eronia cleodora Hübner, 1823	Pieridae
Euphaedra neophron Hopffer, 1855	Nymphalidae
Eurema sp.	Pieridae
Eurytela dryope Cramer, 1779	Nymphalidae
Euxanthe wakefieldi (Ward, 1873)	Nymphalidae
Graphium angolanus (Goeze, 1779)	Papilionidae
Graphium antheus (Cramer, 1779)	Papilionidae
Graphium colonna (Ward, 1873)	Papilionidae
Graphium kirbyi (Hewitson, 1872)	Papilionidae
Graphium leonidas (Fabricius, 1793)	Papilionidae
Graphium philonoe (Ward, 1873)	Papilionidae
Graphium policenes (Cramer, 1775)	Papilionidae
Graphium polistratus (Grose-Smith, 1889)	Papilionidae
Graphium porthaon (Hewitson, 1865)	Papilionidae
Harma theobene Doubleday, [1848]	Nymphalidae
Hypolimnas anthedon (Doubleday, 1845)	Nymphalidae
Hypolimnas deceptor Trimen, 1873	Nymphalidae
Hypolimnas misippus (Linnaeus, 1764)	Nymphalidae
Junonia hierta (Fabricius, 1798)	Nymphalidae
Junonia natalica Felder, 1860	Nymphalidae
Junonia oenone Linnaeus, 1764	Nymphalidae
Leptosia alcesta (Stoll, [1782])	Pieridae
Libythea labdaca Westwood, 1851	Nymphalidae
Melanitis leda Linnaeus, 1758	Nymphalidae
Mylothris agathina (Cramer, 1779)	Pieridae
Nepheronia thalassina (Boisduval, 1836)	Pieridae
Neptis sp.	Nymphalidae
Papilio constantinus Ward, 1871	Papilionidae
Papilio dardanus Brown, 1776	Papilionidae
Papilio demodocus Esper, 1798	Papilionidae
Papilio nireus Linnaeus, 1758	Papilionidae
Pardopsis punctatissima Boisduval, 1833	Nymphalidae
Phalanta phalantha Drury, 1773	Nymphalidae
Physcaeneura leda Gerstaecker, 1871	Nymphalidae
Pinacopteryx eriphia (Godart, 1819)	Pieridae
Pseudacraea boisduvali (Doubleday, 1845)	Nymphalidae
Pseudacraea lucretia (Cramer, 1775)	Nymphalidae
Salamis anacardii Linnaeus, 1758	Nymphalidae
Salamis parhassus Drury, 1782	Nymphalidae
Tirumala petiverana Doubleday, 1847	Nymphalidae

Appendix 2

SIMPER analysis for butterfly species composition dissimilarities results. Highlighted are species that cumulatively contribute up to 70% of the observed dissimilarities.

Table A2. Butterfly species contributing up to 70% of the observed dissimilarities across the sampled forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in the Arabuko Sokoke forest, Kenya. Where average = the average contribution of a species to the dissimilarity between groups; Sd = standard deviation of the species' contribution, showing variability in how much that species contributes across different sample comparisons; Ratio = the average contribution divided by its standard deviation (average / sd). A higher ratio indicates that the species consistently contributes to dissimilarity (less variable); ava = the average abundance or value of the species in forest A (e.g. *Brachystegia*); avb = the average abundance or value of the species in forest type B (e.g. *Cynometra*); cumsum = the cumulative sum of the contributions up to the current species, usually expressed as a percentage of total dissimilarity explained so far. This helps identify which species collectively contribute to a specified threshold (e.g., 70%); P-value = statistical significance testing the contribution of that species to the dissimilarity, lower values (typically < 0.05) suggest the species contributes significantly to differences between groups.

Species	average	sd	ratio	ava	avb	Cumsum	% of total dissimilarity	P-value
Brachystegia vs Cynometra								
Phalanta phalantha	0.030	0.022	1.330	2.143	1.564	0.049	**4.9**	0.001
Catopsilia florella	0.027	0.023	1.160	1.234	1.646	0.094	**9.4**	0.002
Appias epaphia	0.026	0.022	1.147	1.549	1.828	0.137	**13.7**	0.001
Hypolimnas misippus	0.025	0.021	1.184	0.959	1.151	0.178	**17.8**	0.002
Colotis regina	0.023	0.021	1.121	0.397	1.122	0.217	**21.7**	0.001
Graphium philonoe	0.022	0.019	1.181	0.606	1.190	0.254	**25.4**	0.001
Graphium antheus	0.022	0.020	1.112	1.010	1.018	0.291	**29.1**	0.002
Papilio demodocus	0.022	0.018	1.202	1.106	0.977	0.327	**32.7**	0.006
Neptis sp.	0.022	0.019	1.154	0.884	1.001	0.363	**36.3**	0.001
Junonia oenone	0.020	0.017	1.195	0.958	0.841	0.397	**39.7**	0.031
Colotis euippe	0.018	0.018	1.034	0.784	0.569	0.427	**42.7**	0.025
Eronia cleodora	0.018	0.017	1.080	0.700	0.785	0.458	**45.8**	0.023
Graphium porthaon	0.017	0.017	1.013	0.553	0.665	0.487	**48.7**	0.116
Colotis auxo	0.017	0.015	1.123	0.427	0.739	0.515	**51.5**	0.001
Hypolimnas deceptor	0.017	0.018	0.968	0.000	0.741	0.544	**54.4**	0.001
Coeliades forestan	0.017	0.017	0.974	0.628	0.668	0.572	**57.2**	1.000
Acraea sp.	0.017	0.016	1.072	0.612	0.729	0.600	**60.0**	0.006
Charaxes candiope	0.016	0.015	1.036	0.037	0.705	0.625	**62.5**	0.001
Pardopsis punctatissima	0.015	0.016	0.946	0.552	0.501	0.651	**65.1**	0.001
Bicyclus safitza	0.014	0.016	0.910	0.154	0.616	0.675	**67.5**	0.001
Eurema sp.	0.014	0.023	0.632	0.639	0.117	0.699	**69.9**	0.573
Brachystegia vs Forest edge								
Coeliades forestan	0.033	0.018	1.828	0.628	2.529	0.055	**5.5**	0.001
Hypolimnas misippus	0.021	0.015	1.364	0.959	1.738	0.090	**9.0**	0.183
Junonia oenone	0.021	0.015	1.331	0.958	1.743	0.124	**12.4**	0.022
Papilio demodocus	0.020	0.017	1.142	1.106	1.910	0.158	**15.8**	0.084
Catopsilia florella	0.020	0.019	1.034	1.234	1.415	0.191	**19.1**	0.809
Phalanta phalantha	0.019	0.023	0.846	2.143	2.479	0.224	**22.4**	0.941
Appias epaphia	0.019	0.018	1.063	1.549	2.052	0.255	**25.5**	0.489
Eurema sp.	0.019	0.018	1.052	0.639	1.176	0.287	**28.7**	0.006
Graphium antheus	0.018	0.016	1.126	1.010	1.316	0.317	**31.7**	0.445
Colotis ione	0.018	0.016	1.126	0.295	1.185	0.347	**34.7**	0.001
Colotis euippe	0.017	0.015	1.144	0.784	1.144	0.375	**37.5**	0.261
Eronia cleodora	0.017	0.014	1.182	0.700	1.213	0.403	**40.3**	0.509
Papilio nireus	0.016	0.012	1.310	0.641	1.299	0.430	**43.0**	0.023
Graphium philonoe	0.016	0.015	1.090	0.606	0.993	0.457	**45.7**	0.901
Graphium porthaon	0.016	0.013	1.202	0.553	1.087	0.483	**48.3**	0.660
Danaus chrysippus	0.015	0.014	1.117	0.276	0.991	0.509	**50.9**	0.002
Euphaedra neophron	0.015	0.012	1.261	0.482	1.105	0.534	**53.4**	0.007
Belenois creona	0.015	0.015	1.010	0.191	0.974	0.559	**55.9**	0.001
Papilio constantinus	0.014	0.015	0.930	0.000	0.836	0.584	**58.4**	0.001

Species	average	sd	ratio	ava	avb	Cumsum	% of total dissimilarity	P-value
Neptis sp.	0.014	0.014	1.019	0.884	0.548	0.607	**60.7**	0.957
Charaxes varanes	0.014	0.012	1.104	0.574	0.871	0.630	**63.0**	0.027
Nepheronia thalassina	0.013	0.012	1.125	0.268	0.872	0.652	**65.2**	0.345
Acraea sp.	0.013	0.012	1.058	0.612	0.719	0.674	**67.4**	0.980
Colotis regina	0.012	0.013	0.980	0.397	0.700	0.694	**69.4**	0.974
Brachystegia vs Mixed forest								
Phalanta phalantha	0.026	0.025	1.055	2.143	2.320	0.045	**4.5**	0.073
Hypolimnas misippus	0.022	0.019	1.189	0.959	1.449	0.082	**8.2**	0.029
Catopsilia florella	0.022	0.020	1.114	1.234	1.560	0.120	**12.0**	0.285
Appias epaphia	0.021	0.018	1.195	1.549	2.229	0.155	**15.5**	0.123
Papilio demodocus	0.019	0.018	1.070	1.106	1.518	0.188	**18.8**	0.192
Graphium porthaon	0.019	0.017	1.105	0.553	1.144	0.220	**22.0**	0.008
Graphium antheus	0.018	0.017	1.088	1.010	1.087	0.251	**25.1**	0.285
Eronia cleodora	0.018	0.016	1.147	0.700	1.032	0.281	**28.1**	0.072
Junonia oenone	0.018	0.015	1.226	0.958	0.934	0.311	**31.1**	0.795
Graphium philonoe	0.018	0.015	1.175	0.606	1.201	0.341	**34.1**	0.433
Colotis euippe	0.017	0.014	1.208	0.784	1.142	0.370	**37.0**	0.262
Papilio nireus	0.017	0.015	1.144	0.641	1.185	0.399	**39.9**	0.002
Neptis sp.	0.016	0.015	1.060	0.884	0.926	0.427	**42.7**	0.347
Nepheronia thalassina	0.016	0.015	1.060	0.268	0.940	0.454	**45.4**	0.001
Acraea sp.	0.016	0.015	1.075	0.612	0.999	0.481	**48.1**	0.033
Coeliades forestan	0.016	0.016	1.019	0.628	0.921	0.508	**50.8**	0.999
Eurema sp.	0.016	0.020	0.797	0.639	0.669	0.535	**53.5**	0.332
Belenois thysa	0.015	0.013	1.120	0.265	0.922	0.560	**56.0**	0.001
Papilio constantinus	0.015	0.015	1.008	0.000	0.843	0.585	**58.5**	0.001
Euphaedra neophron	0.013	0.014	0.990	0.482	0.710	0.608	**60.8**	0.403
Charaxes varanes	0.013	0.012	1.078	0.574	0.823	0.630	**63.0**	0.092
Junonia natalica	0.012	0.013	0.953	0.845	1.201	0.651	**65.1**	0.157
Danaus chrysippus	0.012	0.013	0.896	0.276	0.668	0.671	**67.1**	0.424
Colotis auxo	0.012	0.013	0.874	0.427	0.547	0.691	**69.1**	0.831
Cynometra vs Forest edge								
Coeliades forestan	0.030	0.016	1.934	0.668	2.529	0.051	**5.1**	0.001
Phalanta phalantha	0.021	0.018	1.162	1.564	2.479	0.087	**8.7**	0.771
Papilio nireus	0.020	0.009	2.146	0.000	1.299	0.121	**12.1**	0.001
Junonia oenone	0.020	0.015	1.317	0.841	1.743	0.154	**15.4**	0.116
Catopsilia florella	0.020	0.018	1.067	1.646	1.415	0.187	**18.7**	0.849
Papilio demodocus	0.018	0.014	1.349	0.977	1.910	0.218	**21.8**	0.422
Graphium philonoe	0.018	0.015	1.197	1.190	0.993	0.247	**24.7**	0.499
Hypolimnas misippus	0.017	0.014	1.228	1.151	1.738	0.275	**27.5**	0.972
Colotis ione	0.017	0.014	1.153	0.445	1.185	0.303	**30.3**	0.004
Appias epaphia	0.017	0.015	1.129	1.828	2.052	0.331	**33.1**	0.902
Colotis regina	0.016	0.014	1.161	1.122	0.700	0.359	**35.9**	0.153
Eurema sp.	0.016	0.015	1.091	0.117	1.176	0.386	**38.6**	0.209
Colotis euippe	0.016	0.014	1.151	0.569	1.144	0.413	**41.3**	0.663
Graphium antheus	0.016	0.014	1.126	1.018	1.316	0.440	**44.0**	0.932
Eronia cleodora	0.015	0.013	1.160	0.785	1.213	0.465	**46.5**	0.968
Danaus chrysippus	0.015	0.013	1.134	0.163	0.991	0.490	**49.0**	0.004
Neptis sp.	0.015	0.014	1.035	1.001	0.548	0.514	**51.4**	0.870
Graphium porthaon	0.014	0.013	1.151	0.665	1.087	0.538	**53.8**	0.931
Euphaedra neophron	0.014	0.011	1.309	0.379	1.105	0.562	**56.2**	0.097
Belenois creona	0.014	0.014	0.994	0.000	0.974	0.586	**58.6**	0.001
Charaxes varanes	0.014	0.012	1.129	0.000	0.871	0.609	**60.9**	0.016
Papilio constantinus	0.013	0.014	0.979	0.000	0.836	0.632	**63.2**	0.003
Acraea sp.	0.013	0.012	1.102	0.729	0.719	0.654	**65.4**	0.982
Hypolimnas deceptor	0.013	0.012	1.014	0.741	0.503	0.675	**67.5**	0.114
Nepheronia thalassina	0.012	0.011	1.141	0.465	0.872	0.695	**69.5**	0.777

Species	average	sd	ratio	ava	avb	Cumsum	% of total dissimilarity	P-value
Cynometra vs Mixed forest								
Phalanta phalantha	0.026	0.019	1.330	1.564	2.320	0.045	**4.5**	0.112
Catopsilia florella	0.021	0.018	1.170	1.646	1.560	0.080	**8.0**	0.604
Papilio nireus	0.020	0.012	1.649	0.000	1.185	0.115	**11.5**	0.001
Hypolimnas misippus	0.020	0.017	1.159	1.151	1.449	0.149	**14.9**	0.425
Colotis regina	0.019	0.017	1.073	1.122	0.429	0.181	**18.1**	0.003
Appias epaphia	0.018	0.014	1.259	1.828	2.229	0.212	**21.2**	0.687
Graphium porthaon	0.018	0.016	1.154	0.665	1.144	0.243	**24.3**	0.048
Graphium philonoe	0.017	0.015	1.162	1.190	1.201	0.273	**27.3**	0.636
Papilio demodocus	0.017	0.014	1.224	0.977	1.518	0.302	**30.2**	0.832
Eronia cleodora	0.017	0.014	1.169	0.785	1.032	0.330	**33.0**	0.417
Neptis sp.	0.017	0.015	1.124	1.001	0.926	0.359	**35.9**	0.267
Junonia oenone	0.017	0.014	1.182	0.841	0.934	0.387	**38.7**	0.990
Colotis euippe	0.017	0.013	1.263	0.569	1.142	0.416	**41.6**	0.492
Graphium antheus	0.017	0.015	1.090	1.018	1.087	0.444	**44.4**	0.857
Acraea sp	0.015	0.014	1.101	0.729	0.999	0.470	**47.0**	0.214
Coeliades forestan	0.015	0.014	1.062	0.668	0.921	0.496	**49.6**	1.000
Nepheronia thalassina	0.015	0.014	1.080	0.465	0.940	0.521	**52.1**	0.023
Belenois thysa	0.014	0.012	1.153	0.444	0.922	0.545	**54.5**	0.002
Papilio constantinus	0.014	0.014	1.025	0.000	0.843	0.569	**56.9**	0.001
Hypolimnas deceptor	0.014	0.014	1.018	0.741	0.513	0.593	**59.3**	0.009
Charaxes varanes	0.014	0.011	1.282	0.000	0.823	0.616	**61.6**	0.026
Colotis auxo	0.013	0.012	1.092	0.739	0.547	0.639	**63.9**	0.202
Bicyclus safitza	0.013	0.013	0.951	0.616	0.447	0.661	**66.1**	0.015
Charaxes candiope	0.012	0.012	1.008	0.705	0.179	0.682	**68.2**	0.001
Euphaedra neophron	0.012	0.012	0.997	0.379	0.710	0.703	**70.3**	0.912
Forest edge vs Mixed forest								
Coeliades forestan	0.025	0.015	1.612	2.529	0.921	0.047	**4.7**	0.003
Junonia oenone	0.018	0.014	1.352	1.743	0.934	0.082	**8.2**	0.648
Phalanta phalantha	0.017	0.019	0.901	2.479	2.320	0.114	**11.4**	0.995
Catopsilia florella	0.017	0.015	1.070	1.415	1.560	0.145	**14.5**	0.998
Eurema sp.	0.015	0.013	1.116	1.176	0.669	0.174	**17.4**	0.471
Colotis ione	0.015	0.014	1.084	1.185	0.662	0.201	**20.1**	0.189
Graphium philonoe	0.015	0.012	1.231	0.993	1.201	0.229	**22.9**	0.995
Colotis euippe	0.014	0.011	1.250	1.144	1.142	0.256	**25.6**	0.994
Eronia cleodora	0.014	0.012	1.185	1.213	1.032	0.283	**28.3**	0.995
Hypolimnas misippus	0.014	0.013	1.091	1.738	1.449	0.310	**31.0**	1.000
Graphium antheus	0.014	0.013	1.103	1.316	1.087	0.336	**33.6**	0.999
Graphium porthaon	0.013	0.012	1.115	1.087	1.144	0.361	**36.1**	0.999
Papilio demodocus	0.013	0.013	1.005	1.910	1.518	0.387	**38.7**	0.997
Danaus chrysippus	0.013	0.012	1.097	0.991	0.668	0.411	**41.1**	0.143
Appias epaphia	0.013	0.011	1.117	2.052	2.229	0.434	**43.4**	1.000
Acraea sp.	0.013	0.011	1.104	0.719	0.999	0.458	**45.8**	0.991
Belenois creona	0.012	0.013	0.995	0.974	0.175	0.482	**48.2**	0.001
Euphaedra neophron	0.012	0.010	1.154	1.105	0.710	0.504	**50.4**	0.948
Papilio constantinus	0.012	0.011	1.054	0.836	0.843	0.526	**52.6**	0.087
Nepheronia thalassina	0.012	0.011	1.046	0.872	0.940	0.548	**54.8**	0.919
Neptis sp.	0.011	0.011	1.056	0.548	0.926	0.570	**57.0**	1.000
Belenois thysa	0.011	0.010	1.109	0.329	0.922	0.592	**59.2**	0.520
Graphium colonna	0.011	0.011	0.993	0.771	0.577	0.612	**61.2**	0.581
Charaxes varanes	0.011	0.009	1.157	0.871	0.823	0.633	**63.3**	0.960
Colotis regina	0.011	0.011	0.964	0.700	0.429	0.653	**65.3**	0.998
Junonia natalica	0.010	0.011	0.912	0.992	1.201	0.671	**67.1**	0.929
Melanitis leda	0.010	0.009	1.035	0.648	0.574	0.689	**68.9**	0.174
Hypolimnas deceptor	0.010	0.011	0.859	0.503	0.513	0.707	**70.7**	0.882

Supplementary material 1

Suppl. figures S1–S3

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Data type: pdf

Explanation note: **figure S1.** Frequency ranking of butterfly species abundance within the forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in Arabuko Sokoke Forest, Kenya. **figure S2.** Abundance proportions of butterfly species with monophagous, oligophagous and polyphagous larval feeding habits across the four forest types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in Arabuko Sokoke Forest, Kenya. **figure S3.** Butterflies in Arabuko Sokoke Forest, in the mixed forest vegetation type, feeding from elephant dung during the field sampling in the dry season. Photo credits: Maria Fungomeli.

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