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COMPARATIVE STUDY OF BUTTERFLY (LEPIDOPTERA: PAPILIONOIDEA) COMMUNITIES IN MONOCULTURE AND POLYCULTURE OIL PALM SMALLHOLDINGS IN JOHOR, MALAYSIA

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ABSTRACT

Conversion of tropical forests to oil palm (*Elaeis guineensis*) plantations is a primary driver of biodiversity loss. Polyculture farming is widely promoted as a mitigation strategy, yet empirical evidence from smallholder systems, particularly for sensitive bioindicator taxa like butterflies, remains limited. This study aimed to bridge this knowledge gap by directly comparing butterfly communities in adjacent monoculture and polyculture smallholder plantations. We investigated butterfly abundance, species richness, and community composition between July 2024 to January 2025 in a smallholder monoculture and polyculture site integrated with fruit crops and livestock in Johor, Malaysia. Butterflies were sampled using baited traps and aerial net surveys along standardized transects. Diversity was quantified using the Shannon (H') and Evenness (E') indices, and community similarity was assessed using Jaccard Similarity Index. Habitat characterization included measurements of canopy cover, tree density, shrub density, and herbaceous cover. A total of 381 individuals from 48 species and five families of butterflies were recorded. Habitat assessment revealed a high degree of structural uniformity between the two sites, with no significant differences in canopy cover, tree density and understorey density ($P > 0.05$). Despite the physical uniformity, the polyculture system supported significantly higher butterfly abundance and species richness (38 species; $H' = 2.641$) compared to the monoculture system (32 species; $H' = 2.518$). A Kruskal-Wallis test confirmed a statistically significant difference in butterfly community structure between the

two management systems ($H = 4.379$, $P > 0.05$). The polyculture site was characterized by high abundances of *Elymnias hypermnestra beatrice* (31.56%) and *Junonia almana javana* (19.77%), likely driven by the increased floristic quality of intercropped fruit trees and organic resource from integrated livestock. Our findings demonstrated that butterfly diversity in smallholder landscapes is driven by variety in resources and habitat quality rather than mere structural density. This emphasizes the importance of polyculture and livestock integration as effective tools for sustaining tropical biodiversity in agricultural settings.

Keywords: Butterfly diversity; oil palm; polyculture; smallholder agriculture; bioindicator

ABSTRAK

Penukaran hutan tropika kepada ladang kelapa sawit (*Elaeis guineensis*) merupakan pemacu utama kemerosotan biodiversiti. Amalan penanaman polikultur dalam ladang kelapa sawit digunakan secara meluas sebagai strategi untuk mengurangkan impak kemerosotan biodiversiti ini. Namun begitu, bukti kukuh dari kawasan sawit yang dimiliki pekebun kecil, terutamanya bagi kumpulan serangga bioindikator seperti kupu-kupu masih terhad. Kajian ini bertujuan untuk merapatkan jurang pengetahuan tersebut dengan membandingkan secara langsung komuniti kupu-kupu di ladang pekebun kecil yang mengamalkan teknik monokultur dan polikultur. Kajian ini mengenalpasti kelimpahan, kekayaan spesies dan komposisi komuniti kupu-kupu di dua ladang kelapa sawit pekebun kecil di Johor bermula pada bulan Julai 2024 hingga Januari 2025. Dua ladang ini ialah ladang monokultur yang hanya menanam kelapa sawit dan ladang polikultur yang disepadukan dengan tanaman buah-buahan dan haiwan ternakan. Persampelan kupu-kupu menggunakan gabungan perangkap berumpan dan jaring sauk. Kepelbagaian kupu-kupu dinilai menggunakan Indeks Shannon (H') dan Kesamarataan (E'), manakala keserupaan komuniti dinilai dengan Indeks Jaccard. Pencirian habitat merangkumi pengukuran litupan kanopi, kepadatan pokok, kepadatan semak dan litupan herba. Sejumlah 381 individu daripada 48 spesies dan lima famili telah direkodkan. Penilaian habitat menunjukkan tahap keseragaman struktur yang tinggi antara kedua-dua tapak, tanpa perbezaan signifikan dalam litupan kanopi, kepadatan pokok dan kepadatan tumbuhan bawah ($P > 0.05$). Di sebalik keseragaman fizikal ini, sistem polikultur menyokong kelimpahan dan kekayaan spesies kupu-kupu yang secara signifikan lebih tinggi (38 spesies; $H' = 2.641$) berbanding sistem monokultur (32 spesies; $H' = 2.518$). Ujian Kruskal-Wallis mengesahkan perbezaan signifikan secara statistik dalam struktur komuniti kupu-kupu antara dua sistem pengurusan tersebut ($H' = 4.379$, $P > 0.05$). Tapak polikultur dicirikan oleh kelimpahan tinggi *Elymnias hypermnestra beatrice* (31.56%) dan *Junonia almana javana* (19.77%), yang berkemungkinan didorong oleh peningkatan kualiti floristik pokok buah-buahan dan sumber organik daripada ternakan bersepadu. Penemuan kajian ini menunjukkan bahawa kepelbagaian kupu-kupu dalam landskap pekebun kecil didorong oleh jenis sumber makanan dan kualiti habitat, bukannya sekadar kepadatan struktur. Ini menekankan kepentingan integrasi polikultur dan ternakan sebagai cara yang berkesan untuk mengekalkan biodiversiti tropika dalam kawasan pertanian.

Kata kunci: Kepelbagaian kupu-kupu; kelapa sawit; polikultur; pertanian pekebun kecil; bioindikator

INTRODUCTION

Conversion of primary and secondary forest into agricultural lands is currently one of the major threats to global biodiversity (Kadoya et al. 2022). The expansion of oil palm (*Elaeis*

guineensis) cultivation is a primary driver of biodiversity decline across tropical Southeast Asia over the past few decades (Vijay et al. 2016). Expansive areas of natural forests have been converted to agricultural plantations, and the crop contributes substantially to the economy of the countries that produce it. This is particularly true in Malaysia, where this industry is a cornerstone of the economy. As of 2024, the Malaysian Palm Oil Board (MPOB) reported 5.6 million hectares of oil palm plantations, producing 19.33 million tonnes of oil annually (MPOB 2024). Within Peninsular Malaysia, 10.89 million tonnes of oil are produced annually, with Johor being one of the major producing states.

The vast expansion of oil palm monoculture plantations has raised concerns about its impact towards biodiversity. Studies have shown that converting primary forests into monoculture plantations such as oil palm results in significant ecological costs, including habitat fragmentation (Vijay et al. 2016), diminished carbon sequestration (Murphy 2024), and the isolation of wildlife populations (Mohd-Azlan et al. 2019). These changes disproportionately affect sensitive taxa that rely on complex forest structures, potentially leading to localized extinctions and reduced genetic diversity. For instance, compared to forests, oil palm plantations are known to foster a lower species richness of birds, butterflies and mammals (Harich & Treydte 2016; Miller III et al. 2011; Teuscher et al. 2015).

While industrial-scale plantations are often characterized by vast monocultures, the smallholder sector presents a different landscape. Globally, 27.3% of oil palm plantation area is managed by smallholder (Descals et al. 2021). Smallholder systems are often more heterogeneous and are frequently promoted as potential "wildlife-friendly" matrices (Azhar et al. 2015). Specifically, polyculture practices, the integration of multiple crops or livestock within oil palm stands, are widely advocated as a strategy to mitigate biodiversity loss. It is theorized that polycultures enhance species diversity by increasing structural complexity, improving soil fertility, and providing natural pest regulation, thereby reducing the need for chemical pesticides that harm non-target pollinators (Iverson et al. 2014).

Despite the theoretical benefits of polyculture, empirical evidence remains inconsistent, particularly regarding how these systems influence sensitive bioindicators like butterflies. Butterflies are ideal indicators of ecosystem health due to their high sensitivity to microclimatic shifts and their reliance on specific host plants (Bonebrake et al. 2010). While some studies suggest that polycultures support higher biodiversity (Iverson et al. 2014), it remains unclear whether the farming system itself (monoculture or polyculture) is the primary driver of diversity, or if local habitat characteristics, such as canopy openness, understory vegetation, and specific resource availability, play a more decisive role.

In Johor Malaysia, smallholder oil palm cultivation is expanding rapidly, yet there is a critical lack of understanding regarding how different management practices impact local biodiversity. This study aims to bridge this gap by comparing butterfly assemblages between monoculture and polyculture smallholdings. To achieve this objective, the study aimed to address three research questions related to butterfly diversity in oil palm agricultural systems: (1) Does the transition from a monoculture to a polyculture system in smallholder plantations result in a significant increase in butterfly species richness and abundance? (2) How does the species assemblage of butterflies shift between monoculture and polyculture sites, and which specific species are associated with each habitat? (3) Are local environmental factors such as canopy openness, livestock presence, and fruit availability more influential in predicting butterfly community structure than the farming system?

MATERIALS AND METHODS

Study Area

The study was conducted in smallholder oil palm plantations in Parit Sulong, Batu Pahat, Johor (1.9660° N, 102.8955° E) that were mostly managed by local villagers (Figure 1). Both sampling sites covered a total area of 5.6 ha. Each core sampling site measured 2.0 hectares, while the remaining area consisted of sections that were not included in the sampling due to inaccessibility. These sampling sites also shared similar topography and climatic conditions. The terrain has no significant variation in elevation and is mostly flat. The distance between the two plantations is approximately 1 kilometre.

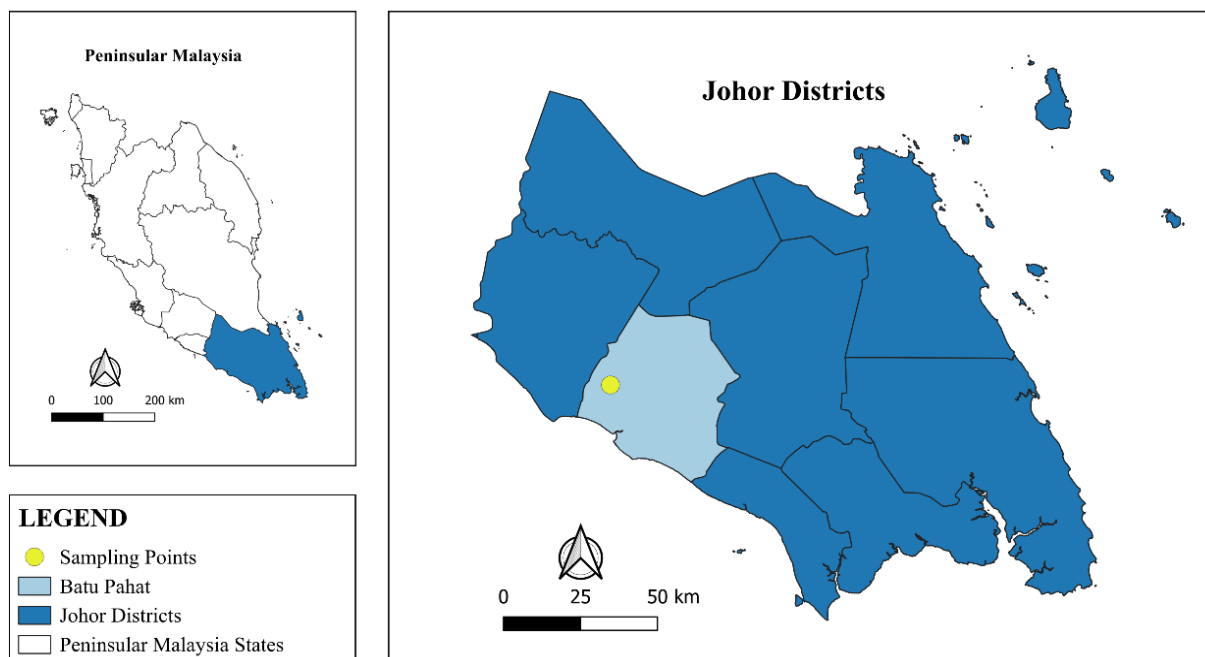


Figure 1. Map of Batu Pahat district in Johor, Malaysia. The yellow dot signifies the sampling location of the monoculture and polyculture sites within the district. The map of sampling sites was visualized using QGIS (QGIS 2025)

Following the classification by Asmah et al. (2017), the study sites were categorized into two systems: monoculture and polyculture. The monoculture system consisted exclusively of oil palm, (*Elaeis guineensis*) with palms approximately 15-20 years old, featuring an open canopy and a managed understory dominated by grasses and ferns, mimicking the conditions of large-scale industrial plantations. In contrast, the polyculture system was an integrated plantation consisting of oil palms aged between 2 and 30 years, intercropped with various fruit trees, including soursop (*Annona muricata*), lime (*Citrus aurantifolia*), mango (*Mangifera indica*), coconut (*Cocos nucifera*), and chilies (*Capsicum annum*). This site also featured integrated livestock, including domestic goats (*Capra hircus*), chickens (*Gallus gallus*), and turkeys (*Meleagris* sp.). The wide age range in oil palm may influence canopy structure, light availability, and vegetation characteristics, which could in turn affect butterfly diversity. Although palm age was not controlled, sampling was conducted across the site to capture its inherent habitat heterogeneity, thereby providing a representative assessment of butterfly diversity.

The study was conducted over a seven-month period from July 2024 to January 2025. The mean relative humidity during that period was 83.3%, with an average temperature of 24 – 32 °C. Slightly lower temperatures were recorded in December 2024 and January 2025 due to increased rainfall patterns (Malaysia Meteorological Department 2025).

Sampling Design

Butterfly assemblages were monitored using a multi-method sampling approach to maximize species detection. Passive sampling employed 18 baited traps (nine per site) suspended 1.5 m above the ground along a 1-km transect for each site (DeVries et al. 2016). Traps were baited with a fermented mixture of bananas, pineapples, and yeast, and inspected every three hours between 09:00 and 17:00. Active sampling was conducted concurrently using a modified Pollard Walk method (Royer et al. 1998) along the standardized 1-km transect. This involved aerial netting between 09:00 and 17:00 at 18 checkpoints marked at 50-m intervals. Captured specimens were either identified in situ or humanely euthanized for laboratory identification using the diagnostic keys from Corbet et al. (2020). To prevent double counting, all released butterflies were marked on the hindwing with a permanent marker (Habel et al. 2025). Any recaptured individuals that were marked were excluded from subsequent analyses. Sampling was conducted for at least five days per transect per month.

Habitat Attributes

Habitat attributes were measured to identify potential drivers of butterfly distribution (Evans et al. 2020). Canopy cover was recorded at 100-m intervals using a spherical densiometer. Vegetation structure was assessed at discrete sampling points positioned at 100-m intervals along the transect, with each assessment conducted within a 5-m radius plot, following a modified protocol from Adams et al. (2009). Vegetation was categorized into three strata: trees (>10 cm diameter at breast height, measured at 1.37 m above ground), shrubs (<3 m height with woody stems), and herbs (<1 m height with soft stems). Density for each stratum was scored on a scale of 0 to 5: Absent (0), Sporadic Individuals (1), Several Patches (2), Homogenous Distribution of Isolated Individuals (3), Continuous Coverage with Some Patches (4), and Continuous/Dense Coverage (5) following Blumetto et al. (2019) with modifications.

Statistical Analysis

The resulting dataset was analyzed using Paleontological Statistics (PAST) software version 4.04 (Hammer et al. 2001). To evaluate community structure, the butterfly assemblage was quantified using the Shannon-Weiner Diversity Index (H') and the Species Evenness Index (E). (Magurran 1988). The Shannon-Weiner Diversity Index (H') was chosen to account for both species richness and the relative abundance of individuals within the assemblage. The index is tested for significance using Hutcheson's t-test. Community overlap between the monoculture and polyculture systems was assessed using the Jaccard Similarity Index (J), calculated based on the presence and absence of species at each site. Prior to comparative testing, the dataset was subjected to a Shapiro - Wilk test to verify normality. The Shapiro-Wilk test indicated that the abundance and richness data significantly deviated from normal distribution ($P < 0.05$), which led to the use of non-parametric statistics. To analyze the differences in butterfly species richness and abundance between polyculture and monoculture systems, the Kruskal-Wallis test was used. To evaluate the overall sampling effort, we compared the observed species richness with the Chao1 bias-corrected estimator of species richness using ESTIMATES version 9.1 (Colwell et al. 2004). The Chao1 estimator computes the estimated true species diversity of a sample via an equation. This nonparametric species estimator extrapolates the data to identify what the 'true' number of species may have been (Colwell et al. 1994). Statistical significance was defined at $P < 0.05$.

RESULT AND DISCUSSION

General Assemblage and Taxonomic Composition

A total of 381 individuals were recorded, comprising 48 butterfly species from 36 genera, 16 subfamilies, and five families (Table 1). The family Nymphalidae exhibited the highest species richness with 23 species, followed by Hesperidae (eight species), Pieridae (six species), Lycaenidae (6 species), and Papilionidae (5 species). In terms of management systems, the polyculture smallholding supported higher butterfly species richness (38 species) compared to the monoculture system (32 species). Both plantation types displayed similar family-level composition, with all five families represented at each site. However, the species composition varied between the two habitats, with 10 species found exclusively in the monoculture plantation and 16 species recorded exclusively in the polyculture system.

Table 1. List of butterflies sampled at the monoculture and polyculture sites

Family	Scientific Name	No of Individuals (Monoculture)	No of Individuals (Polyculture)
Papilionidae	Subfamily: Papilioninae		
	<i>Papilio memnon agenor</i> Linnaeus, 1758		1
	<i>Papilio demolion demolion</i> Cramer, [1776]		4
	<i>Papilio demoleus malayanus</i> Wallace, 1865		2
	<i>Papilio polytes romulus</i> Cramer, [1775]	1	
	<i>Graphium agamemnon agamemnon</i> (Linnaeus, 1758)	1	
Pieridae	Subfamily: Pierinae		
	<i>Delias hyparete metarete</i> Butler, [1879]	1	2
	<i>Appias olferna olferna</i> Swinhoe, 1890	6	20
	<i>Leptosia nina nina</i> (Fabricius, 1973)	9	11
	Subfamily: Coliadinae		
	<i>Eurema hecabe hecabe</i> (Moore, 1886)	1	6
	<i>Eurema andersonii andersonii</i> (Moore, 1886)		2
<i>Catopsilia pyranthe pyranthe</i> (Linnaeus, 1758)		2	
Nymphalidae	Subfamily: Danainae		
	<i>Ideopsis similis persimilis</i> (Moore, 1879)		2
	<i>Ideopsis vulgaris macrina</i> (Fruhstorfer, 1904)	1	3
	<i>Euploea midamus chloe</i> (Guerin-Meneville, 1843)		1
	<i>Euploea mulciber mulciber</i> (Cramer, [1777])		2
	Subfamily: Satyrinae		
	<i>Elymnias hypermnestra beatrice</i> Fruhstorfer, [1902]	54	83
	<i>Mycalesis horsfieldii hermana</i> Fruhstorfer, 1908	2	
	<i>Mycalesis visala phamis</i> Talbot & Corbet, 1939	1	1
	<i>Mycalesis mineus marcomalayana</i> Fruhstorfer, 1911	6	3
	<i>Mycalesis perseus cepheus</i> Butler, 1867	2	7
	<i>Ypthima newboldi</i> Distant, 1882	1	
	Subfamily: Morphinae		
	<i>Amathusia phidippus phidippus</i> (Linnaeus, 1763)	4	3
	Subfamily: Heliconiinae		
	<i>Acraea terpsicore</i> (Linnaeus, 1758)	4	3
	Subfamily: Nymphalinae		
	<i>Junonia almana javana</i> C. Felder, 1862	3	52
	<i>Hypolimnas bolina bolina</i> (Linnaeus, 1758)	1	2
	Subfamily: Biblidinae		
	<i>Ariadne ariadne ariadne</i> (Linnaeus, 1763)	1	
	Subfamily: Limentidinae		
	<i>Athyma asura idita</i> Moore, 1858		1
<i>Neptis hylas papaja</i> Moore, [1875]	1	2	
<i>Moduza procris milonia</i> (Fruhstorfer, 1906)		2	

Family	Scientific Name	No of Individuals (Monoculture)	No of Individuals (Polyculture)
	<i>Euthalia aconthea gurda</i> Fruhstorfer, 1906	1	2
	<i>Parthenos sylvia lilacinus</i> Butler, [1879]	1	
	<i>Tanaecia palguna consanguinea</i> Distant, 1886	1	1
	<i>Tanaecia iapis puseda</i> (Moore, [1858])	1	1
	<i>Tanaecia munda waterstradti</i> Corbet, 1941		1
Lycaenidae	Subfamily: Polyommatainae		
	<i>Jamides yehi</i> Eliot, 1995		1
	<i>Jamides celeno aelianus</i> (Fabricius, 1793)	1	4
	Subfamily: Lycaeninae		
	<i>Lampides boeticus</i> (Linnaeus, 1767)		1
	<i>Spindasis lohita senama</i> Seitz, 1926	1	
	Subfamily: Miletinae		
	<i>Allotinus unicolor unicolor</i> C. & R. Felder, [1865]		1
	Subfamily: Theclinae		
	<i>Hypolycaena thecloides thecloides</i> C & R Felder, 1860	3	5
Hesperiidae	Subfamily: Coeliadinae		
	<i>Badamia exclamationis</i> (Fabricius, 1775)	1	
	Subfamily: Hesperinae		
	<i>Suastus gremius gremius</i> (Fabricius, 1798)	1	
	<i>Iambrix salsala salsala</i> (Moore, [1866])	2	12
	<i>Oriens gola pseudolus</i> (Mabille, 1883)		1
	<i>Potanthus omaha omaha</i> (W. H. Edwards, 1863)	2	9
	<i>Telicota augias augias</i> (Linnaeus, 1763)		1
	<i>Cephrenes acalle niasicus</i> (Plotz, 1886)	2	6
	<i>Pelopidas conjunctus conjunctus</i> (Herrich-Schaffer, 1869)	1	
	TOTAL	118	263

Evaluation of sampling effort using the Chao1 estimator indicated that the observed richness represented approximately 72.72% of the ‘true’ species richness for the monoculture system and 63.33% for the polyculture system. For the monoculture system, the estimator stabilized after 44 samples were pooled, whereas the polyculture system required 60 pooled samples to reach stabilization. Therefore, we can conclude that the estimated true species richness in the polyculture system was higher than in the monoculture system, estimated true species richness for the polyculture system is higher than the monoculture system.

Table 2. Comparison of diversity indices between monoculture and polyculture systems

Diversity Index	Polyculture	Monoculture
Shannon–Wiener Index (H')	2.641	2.518
Evenness (E)	0.369	0.388

Analysis of the community structure indicates that the polyculture smallholding supported a slightly higher level of diversity compared to the monoculture site. The Shannon–Wiener Index (H') was notably higher in the polyculture system (H' = 2.641) compared to the monoculture system (H' = 2.518). However, Hutcheson's t-test showed no statistically significant difference in diversity between the two sites (t = -1.05, P < 0.05). Conversely, species evenness (E) was slightly higher in the monoculture site (E = 0.388) compared to the polyculture site (E = 0.369). These relatively low evenness values across both systems reflect

the high dominance of a few prolific species which influenced the overall distribution of individuals.

The butterfly assemblage in the monoculture system was dominated by a single species namely *Elymnias hypermenstra beatrice* Fruhstorfer, [1902] (45.76%). Alternatively, the butterfly assemblage in the polyculture system was dominated by three species: *E. hypermenstra beatrice* (31.56%), *Junonia almana javana* C. Felder, 1862 (19.77%) and *Appias olferna olferna* Swinhoe, 1890 (7.6%). This is not surprising since *E. hypermenstra beatrice* is known to be the commonest and most widespread representative from the genus *Elymnias*, with its larvae known to feed on the leaves of coconut and oil palm (Corbet et al. 2020). A total of 22 species (45%) were recorded as common to both habitat types. The Kruskal-Wallis test confirmed a statistically significant difference between the monoculture and polyculture butterfly communities ($H = 4.379$, $P < 0.05$) (Figure 2). This result suggests that management practices associated with polyculture farming in smallholder plantations may positively influence local butterfly diversity.

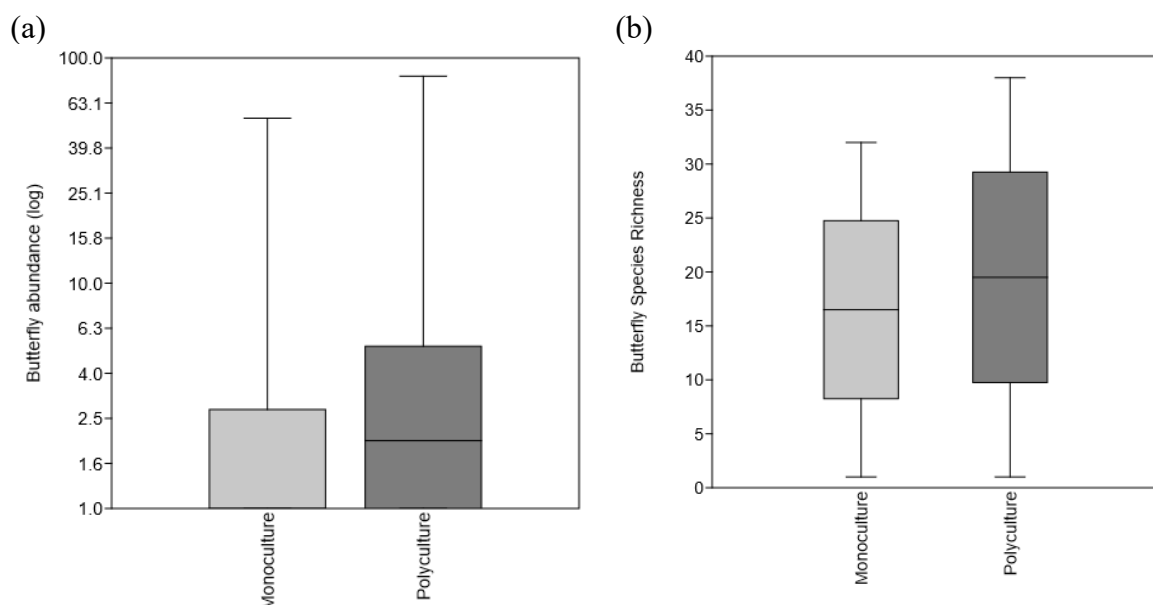


Figure 2. Box plots showing the (a) butterfly abundance and (b) species richness in monoculture and polyculture systems. Significant difference was detected in both response variables between agricultural practice ($P < 0.05$)

The observed pattern of higher butterfly diversity in the polyculture system compared to the monoculture system aligns with findings by Zaki et al. (2023), who demonstrated that agroforestry orchards support significantly richer butterfly assemblages than simplified rubber or oil palm plantations. Our results corroborate the growing body of evidence suggesting that the integration of multiple crops and livestock creates a more ecologically complex matrix, which in turn facilitates higher species richness (Asmah et al. 2017; Lemaire et al. 2014; Miller et al. 2011; Teuscher et al. 2015). Conversely, the trend toward specialized, separated crop and livestock enterprises that is typical of industrial monocultures has been linked to widespread negative consequences for tropical biodiversity (Franzluebbers & Martin 2022). As agricultural intensification continues to rise, the abandonment of integrated, small-scale farming practices poses a severe threat to the long-term sustainability of biodiversity in oil palm-dominated landscapes (Zaehring et al. 2021).

The presence of 16 species exclusive to the polyculture site may be associated with the intercropped fruit trees (*Annona muricata*, *Citrus aurantifolia*, *Mangifera indica*), which could provide a wider range of larval host plants and adult nectar sources compared to the monoculture plantation. For instance, the relatively high abundance of *J. almana javana* (19.77% of the polyculture assemblage) may be linked to the increased floral diversity and more open understory conditions in the polyculture system, as sun-loving nymphalid butterflies are often associated with nectar-rich and vegetation-diverse habitats (Rossato et al. 2025). In contrast, the monoculture system was dominated by *E. hypermnestra beatrice* (45.76%), a resilient generalist. Overall, the high dominance and lower species richness observed suggest that monoculture plantations may act as a filter, favoring only a small number of generalist species that can tolerate resource-poor environments (Vujanović et al. 2025). However, since host plants and nectar resources were not directly measured, these explanations should be interpreted as possible associations rather than confirmed causes.

Habitat Attributes

In terms of habitat characterization, there is a high degree of structural uniformity between the two sites. There was no statistically significant difference in the mean tree density, shrub density, and herbaceous cover of both monoculture and polyculture sites (Table 2). Similarly, although the polyculture site showed a slightly higher mean canopy cover (83.39±3.14%) than the monoculture site (80.10±2.14%), this difference was not statistically significant (Mann-Whitney U: $P < 0.05$). These results suggest that the two types of plantation management systems have similar vegetation density and light availability, which are often cited as primary drivers of insect community assembly (Morpurgo et al. 2024).

Table 3. Habitat attributes of monoculture and polyculture systems

Habitat Attribute	Monoculture	Polyculture	<i>P-value</i>
Mean Canopy Cover (%)	80.11±2.14	83.40±3.15	$P > 0.05$
Mean Tree Density Score	2.58±0.19	2.58±0.19	$P > 0.05$
Mean Shrub Density Score	0.50±0.41	0.33±0.24	$P > 0.05$
Mean Herbaceous Cover Score	3.6±1.4 x 10 ⁻¹⁵	3.6±1.4 x 10 ⁻¹⁵	$P > 0.05$

Our findings suggest that habitat structure alone is not enough to determine the butterfly diversity within an area. While the physical density of trees, shrubs and herbs was statistically identical for both sites ($P < 0.05$), the butterfly community was significantly more abundant and diverse in the polyculture system ($P = 0.027$). This clearly indicates that butterfly assemblages in smallholder landscapes are determined by habitat quality and floristic composition rather than just structural density (Azhar et al. 2015).

In the monoculture site, the plantation was mostly composed of *Elaeis guineensis*, therefore offering limited niches for insects such as butterflies and other non-pest arthropods (Turner & Foster 2009). In contrast, the same tree density within the polyculture site represented a more diverse vegetation composition in terms of species including *Mangifera indica*, *Annona muricata* and *Citrus aurantifolia*. Throughout their lifecycle, butterflies require a suite of distinct resources, ranging from specific larval host plants to diverse adult nectar sources (Corbet 2000). For butterflies, the polyculture system represents a resource-rich environment that satisfies these complex requirements across multiple life stages. The availability of these specific resources has been linked directly to the abundance of adult butterflies in both natural and anthropogenic ecosystems (Choudhary & Chishty 2020).

Common oil palm species, such as *E. hypermnestra*, rely heavily on flowering plants during their adult stage (Wei et al. 2017). The presence of both naturally occurring understory plants and intentionally planted fruit trees provides a variety of habitat niches and food sources that accommodate a wider range of species, a conclusion supported by the significantly higher richness observed in our polyculture site.

Beyond nectar dependency, tropical butterfly assemblages include species within the fruit-feeding guild that obtain nutrition from rotting fruit, fermenting sap, and animal waste (DeVries et al. 2016). The integration of livestock, such as goats and poultry, within the polyculture system introduces these extra resources in the form of manure and other organic resources. Such resources are largely absent in monoculture systems, which are often managed for clear understories through herbicide application. This lack of resource heterogeneity in monocultures may lead to a general reduction in biodiversity, allowing only a few resilient, generalist species to thrive in a simplified environment (Sánchez-Dávila et al. 2024). Our study supports the conclusion that polyculture systems differ significantly in butterfly diversity due to vegetation heterogeneity and resource diversity, rather than physical vegetation density alone.

Study Limitations

It is important to acknowledge the limitations of our sampling methodology. The use of fruit-baited traps is known to introduce a taxonomic bias, primarily attracting species within the fruit-feeding guild (Cleary et al. 2004). Although this was supplemented by active aerial netting, a large proportion of the captured individuals (e.g., *E. hypermnestra*) were obtained via baited traps. Furthermore, the traps were positioned 1.5 meters above ground level. This standardized height may fail to sample species that exclusively occupy the higher canopy or the extreme lower strata, potentially leading to an underestimation of the 'actual' species richness (Schulze et al. 2001). Future studies should consider multi-strata sampling to capture the full vertical profile of butterfly diversity in integrated oil palm systems.

CONCLUSION

The results of the present study highlight that polyculture smallholdings serve as superior biodiversity reservoirs compared to monoculture systems. By demonstrating a significant increase in butterfly abundance and richness despite statistically identical vegetation density and canopy cover, this research indicates diverse fruit trees and integrated livestock are the true drivers of community assembly. Our findings also suggest that the functional complexity provided by a varied hostplant is more critical for sustaining sensitive bioindicators than mere structural density.

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AUTHORS DECLARATION

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Conflict of Interest

The authors declare no competing interests. The authors have no conflict of interest to declare that are relevant to the content of this article.

Ethics Declaration

No ethical issue required for this research.

Data Availability Statement

The authors confirm that the data supporting the findings of this study are available within the supplementary materials.

Author Contributions

Kamisah Suhaili, Siti Aisyah Adnan and Umi Syafiqah Ahmad Fahmi were responsible for the conceptualization, methodology, investigation and data curation for this study, as well as preparing the original draft of the manuscript. Muhammad Haziq Ismat Mohamad Rais, Adlil Ikram Sharuddin assisted in data collection and identification. Muhammad Hafizurridwan Mohd Hisam assisted in data curation, species identification and formal analysis of the study. Mahadimenakbar Mohamed Dawood provided co-supervision and contributed to conceptualization, methodology, and funding acquisition for this study, as well as review and editing of the manuscript. Aqilah Awg Abdul Rahman as the main supervisor contributed to the overall supervision of the project, including conceptualization, methodology development, project administration, writing, review and editing of the manuscript.

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