RESEARCH ARTICLE

How do management decisions impact butterfly assemblages in smallholding oil palm plantations in Peninsular Malaysia?

Martina F. Harianja[1] | Jake Stone[1] | Wan Z. W. Mamat[2] | Muhamad A. Hadi[2] | Sarah H. Luke[1,3] | Badrul Azhar[2,4] | Edgar C. Turner[1]

[1]Department of Zoology, University of Cambridge, Cambridge, UK

[2]Department of Forestry Science and Biodiversity, Faculty of Forestry and Environment, Universiti Putra Malaysia, Serdang, Selangor, Malaysia

[3]School of Biosciences, University of Nottingham, Nr Loughborough, UK

[4]Biodiversity Unit, Institute of Bioscience, Universiti Putra Malaysia, Serdang, Selangor, Malaysia

Correspondence
Martina F. Harianja
Email: mfh46@cam.ac.uk;
martina.f.harianja@gmail.com

Abstract

1. In the world's leading palm oil-producing countries (Indonesia and Malaysia), smallholders make up about 40 per cent of total oil palm plantation area. Management in smallholdings can be highly variable, ranging from intensive monoculture to polyculture systems, especially in the earlier years of cultivation when open canopies allow a variety of understorey crop types to be grown alongside oil palm. Currently, many plantations in the region are mature and due to be replanted, which is likely to have substantial impacts on the ecosystems within them, but studies investigating the impacts of alternative post-replanting management strategies in smallholder plantations are lacking.

2. We investigated the impacts of replanting and choice of crop management following replanting (growing oil palm as a monoculture or polyculture) on habitat structure and complexity, and on the abundance, richness and composition of butterfly assemblages in smallholding oil palm plantations in Banting, Selangor, Malaysia. We also assessed the direct effects of habitat structure and complexity on butterfly assemblages. Butterflies are likely to be a valuable indicator group for monitoring the impacts of management practices on biodiversity as butterfly species also show a range of sensitivities to habitat disturbance, with some being vulnerable to change, but others being common in plantations. They are also a functionally important group that pollinate wild plants, are prey for larger species and are common in tropical systems.

3. Across 27 plantations, we recorded 1227 butterflies from 5 families, 46 genera and 56 species. Habitat structure and complexity differed between management decisions (mature monoculture, immature monoculture, immature polyculture), although many environmental parameters overlapped. We found no significant differences in species richness, density and assemblage composition of butterflies between management decisions. However, changes in local environmental conditions, such as an increase in the coverage of understorey vegetation, increased the abundance of butterflies.

4. *Synthesis and applications*. Our findings suggest that replanting oil palm and choice of mono or polyculture have relatively few effects on butterflies, but management for specific features in plantations could benefit butterfly assemblages.

1 | INTRODUCTION

About 11% of the global land surface is used for crop production, and agricultural practices have driven the loss or reduction in biodiversity (Raven & Wagner, 2021). Agricultural intensification has resulted in the destruction of habitats for wildlife through habitat simplification, fragmentation of remaining natural habitats, as well as negative impacts through inputs of fertilisers, herbicides and pesticides (Raven & Wagner, 2021). As a result, a wide range of terrestrial and aquatic taxa have experienced reductions in diversity, abundance and biomass (Bar-On et al., 2018; Davison et al., 2021). Within established agricultural areas, farmlands that apply conservation management strategies can have higher biodiversity than those that do not (Estrada-Carmona et al., 2022). These practices may also maintain ecosystem services that support yield. For example, plantations with higher complexity have higher species diversity, level of fruit set (Mediterranean cereal fields, Dainese et al., 2017), fruit production (Mexican coffee plantations, Vergara & Badano, 2009) and pest control (annual crop fields in South Korea, Martin et al., 2013).

A good case study for this is oil palm, which had a global cultivated area of 19.5 million hectares in 2019 (Meijaard et al., 2020), the expansion of which has resulted in widespread forest loss (Gaveau et al., 2016). Previous studies have found that management can benefit biodiversity in oil palm and maintain ecosystem services such as decomposition (Ashton-Butt et al., 2019), hence potentially benefitting production. For example, reduced herbicide spraying can increase the cover and complexity of understorey vegetation, which can provide habitat for a wider range of species, reduce extreme temperatures during the heat of the day (Luke et al., 2020) and provide food resources to support higher abundances of several animal taxa, such as leopard cats (Hood et al., 2019), spiders (Spear et al., 2018), butterflies (Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Ps, et al., 2023), assassin bugs (Stone et al., 2023) and soil arthropods (Ashton-Butt et al., 2018).

Oil palm is replanted after 25 years, when yields begin to drop, and harvesting becomes less efficient, changing the structure and environmental conditions within plantations (Snaddon et al., 2013). However, few studies have assessed the impacts of replanting on taxa and ecosystem functions, with those that have identified a decrease in species richness and abundance of frogs (Kurz et al., 2016), and an altered assemblage composition of soil macrofauna (Ashton-Butt et al., 2019) and spiders (Pashkevich et al., 2021). However,

some ecosystem functions, such as dung removal and mesofauna feeding activity, remained unaffected, with herbivory levels being higher in recently replanted (1–4 years) than in mature plantations (23–30 years) (Woodham et al., 2019).

In Indonesia and Malaysia, the world's major palm oil producers, smallholders make up about 40 per cent of the total oil palm area (Wild Asia, 2012). Unlike industrial plantations, smallholders often plant other crops alongside oil palm (polyculture) to gain additional income or as cash crops (Yahya et al., 2017). This is particularly done when oil palm is immature (Shuhada et al., 2020; Yahya et al., 2017), during which an open canopy allows understorey crops to be cultivated. Since polyculture plantations are more diverse in crop species, this could support more wildlife through provision of a wider range of food sources, nesting sites and refuges. Alternatively, it could be that polycultures result in a larger area of understorey being devoted to crops, more intensive management, lower levels of non-crop vegetation and therefore lower levels of biodiversity. The few studies that have investigated the effects of mono versus polyculture oil palm on biodiversity have found varying results (e.g. Asmah et al., 2017; Syafiq et al., 2016; Yahya et al., 2017). For example, species richness of fruit-feeding butterflies did not differ between oil palm monoculture and polyculture (plantations of 2–30 years old [Asmah et al., 2017]), while species richness of birds (Yahya et al., 2017) and frugivorous bats (Syafiq et al., 2016) was higher in polyculture (plantations aged between 2 and 35 years old in both Syafiq et al., 2016 and Yahya et al., 2017).

Within oil palm, invertebrates support a wide range of ecosystem services (e.g., nutrient cycling, biological control and pollination [Dislich et al., 2017]). Butterflies are among the invertebrate groups that pollinate flowering weeds, as well as being prey items for many predators. Owing to their sensitivity to environmental conditions, they are often used as bioindicators of environmental change (Kleiman et al., 2021; Koh, 2007). Previous studies have shown that polyculture farming (Asmah et al., 2017) and maintaining understorey complexity within plantations (Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Ps, et al., 2023; Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Sudharto, et al., 2023) can increase butterfly abundance in oil palm, but no study has yet investigated the impacts of replanting as a monoculture or polyculture on butterfly populations.

Using first- and second-generation oil palm smallholdings in Peninsular Malaysia, we assessed the effects of replanting and alternative replanting decisions (replanting with monoculture versus polyculture oil palm plantations) on the local environment and butterfly assemblages. We asked:

1. How does mature oil palm monoculture (the previous dominant land use in the area) differ from plots replanted with monoculture versus polyculture immature oil palm, in terms of habitat structure and complexity, as well as butterfly density, richness and composition? We hypothesised that mature oil palm would have higher habitat complexity and a reduced temperature range (supported by higher canopy cover [Luskin & Potts, 2011]) than both types of immature plots, supporting higher density and richness and differing composition of butterflies. We hypothesised that immature mono- and polyculture oil palm plantations would differ from each other in habitat complexity, density, richness and composition, but this could be in either direction, depending on the relative benefits of maintaining natural understorey, or growing a range of crops.
2. What is the impact of habitat structure and complexity across management decisions on the density, species richness and assemblage composition of butterflies? We hypothesised that the density, species richness and composition of butterflies would be influenced by resources present, including foodplants and nectar sources.

2 | MATERIALS AND METHODS

2.1 | Study sites

Data were collected between 21 June 2022 and 28 July 2022 from 27 smallholder oil palm plantations in Banting, Selangor, Malaysia (2.788267°N, 101.546651°E). The 27 plantations consisted of nine each of: mature oil palm monoculture (MM01-09), immature monoculture (IM01-09) and immature polyculture (IP01-09) (Figure S1). None of the mature plantations were first-generation oil palm. We were not able to include mature polyculture plots in our study design, as polyculture practices are generally limited to immature oil palm plantations, and there were no mature polyculture plantations within our area. Other crops cultivated in the immature polyculture plantations ranged from bamboo, banana, cassava, coconut, galangal, yam, jackfruit, pineapple and torch ginger. The size of plantations in this study ranged from 0.208 to 1.290 acres (converted to acres from step counts in the field—assessed by walking the perimeter of each plantation). Plots were interspersed across an area of approximately 4.5 by 3.5 km (Figure S1; see Table S1 for plantation details). The authors have been granted permission to conduct research in Malaysia by the Economic Planning Unit (EPU) of Malaysia's Prime Minister's Department (Ref: EPU 40/200/19/3727, MEA 40/200/19/3705). No additional ethics permission was required to observe butterflies in the field.

2.2 | Data collection

2.2.1 | Habitat structure and complexity

We collected environmental data within plantations as well as from the immediate surrounding area. As habitats were visually similar and were likely to vary in use over short periods of time following cultivation practices, it was not possible to use remote aerial techniques to measure neighbouring habitats. We therefore took the simpler, but robust approach of recording the percentage of neighbouring habitats around focal plantations through systematic perimeter walks (see Figure S2). The same person throughout surveys estimated the length of each perimeter type, which was then converted into a percentage of the total perimeter. Habitat types included were as follows: oil palm monoculture, oil palm polyculture (any combination of crops), housing, road, empty or unused land, grassland or low natural vegetation including ferns and cassava monoculture plantations (Figure S2; Table S2). We recorded the age of oil palm (in years) at each plantation site through interviews with the owners.

When doing the perimeter walks, we counted the number of palms on each side of the plantation, multiplying this to calculate the total number of palms. We also recorded the density of butterfly nectar sources (plants with open flowers as nectar sources, identified using Barnes & Chan, 1990; Fee et al., 2017; Maizatul-Suriza & Idris, 2012; Nobilly et al., 2021; Ya'acob et al., 2022), following the methods of Steffan-Dewenter and Tscharntke (1997): using a scale of 0–5, with $0=$ absent or no flower, $1=<0.5$ flowers per m^2, $2=<1$ flower per m^2, $3=<5$ flowers per m^2, $4=<10$ flowers per m^2 and $5=>10$ flowers per m^2. This assessment was carried out separately for each individual plant species observed, and the average sums were calculated for all flowering wild plants across the four perimeters and central path (see Table S3 and Figure S2).

Environmental data within plantations were collected along a central path (Figure S2), where we recorded crop types present and their total coverage, as well as the density of nectar sources, as above. We also assessed environmental parameters at four $5 \times 5\,m$ sample squares (hereafter, 'sample squares') along the central path (Figure S3). The squares were created using two tape measures laid out in a cross shape with the top of the cross pointing north. Each contained a central sample point (hereafter, 'main sample point') and three sub-sample points, each equidistant from the centre (Figure S4).

Environmental parameters measured within the squares were: percentage vegetation cover (crop, bare ground, fern, other vegetation, oil palm [either a tree or a sapling], leaf litter, cut fronds and other [any type of materials other than the previous categories]), canopy openness, height of the nearest oil palm tree to main sampling point and epiphyte cover on the same palm. Canopy openness was measured using a spherical densiometer (Lemmon, 1956), by standing at the 'main sample point' and taking a reading facing north, south, east and west, before summing and calculating the average percentage canopy openness, following standard

practice. The height of the nearest oil palm tree from the 'main sample point' was measured relative to the person recording environmental parameters (how many times the palm was the height of the recorder, multiplied by the recorder's height [the recorder was the same throughout to ensure consistency]). Epiphyte cover was estimated by eye and recorded as percentage cover of trunk. At each of the three sub-sample points, we measured vegetation height in centimetres, using a measuring stick and then calculated the average for each square. Due to the range of species, we were not able to systematically sample host plants of each butterfly species, but acknowledge that the presence and abundance of these is likely to have a large impact on the density of individual species. However, to provide contextual information, we made a note of host plant species when we encountered them.

2.2.2 | Butterfly surveys

Butterfly surveys were conducted on two days in all plantations between 9 AM and 5 PM and when it did not rain. We stratified the timings of visit to each plantation type by morning, noon and afternoon, and then selected specific plantations at random, to ensure that visit time and weather did not vary systematically between plantation types. During the survey, we walked along the transect and recorded any butterflies with an imagined 5 m × 5 m box in front of the recorder (Figure S5; Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Ps, et al., 2023; Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Sudharto, et al., 2023), covering the entire plantation area. Since our study systems consisted of disturbed habitats containing a restricted subset of species, and butterflies are generally identified from wing patterns, it was fairly straightforward to identify butterflies in the field, and this approach has been used in other related studies (Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Ps, et al., 2023; Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Sudharto, et al., 2023).

Each survey lasted up to two hours. In five cases, owing to lack of time (two immature monocultures [IM01, IM03], one immature polyculture [IP05] and two mature monocultures [MM05, MM06]), plantations were not sampled completely. However, in all cases we were careful to be consistent in our survey effort per area, whether completely surveyed or not, allowing us to take incomplete samples into account in our analyses. When we saw a butterfly, we recorded its scientific name. If it could not be identified, we caught the butterfly and put it in a clear Ziplock plastic bag, before taking photographs of the upper- and underside of its wings. We identified butterflies in the field or from these photographs, using guides by Kirton (2020, third edition), which we brought in the field, and Corbet and Pendleburry (2020, fifth edition). We classified the butterfly based on abundance group (common, less common and rare) across Peninsular Malaysia, using descriptions by Corbet and Pendleburry (2020).

2.3 | Statistical analysis

All analyses and visualisations were carried out with R version 4.0.4 (R Core Team, 2021) and R Studio version 2022.07.1+554 (R Studio Team, 2022). To conduct analyses, we used basic R syntax and package 'dplyr' (Wickham et al., 2021), unless specified below. For visualisations (unless specified), we used 'tidyverse' (Wickham et al., 2019), 'cowplot' (Wilke, 2020) and 'gridExtra' (Auguie, 2017).

2.3.1 | Habitat structure and complexity across plantations

Because we did not have an a priori reason for expecting a subset of measured environmental variables to impact butterfly communities, we used principal component analysis (PCA) to reduce the dimensionality among these variables (Jolliffe, 1986) and to visualise environmental conditions across management types. Since butterflies are mobile, we also included the conditions in the neighbouring habitats in our PCA. The parameters we included were: plantation size (in acres), oil palm age (in years), percentage coverage of crops other than oil palm (bamboo, banana, cassava, coconut, galangal, yam, jackfruit, pineapple and torch ginger), percentage coverage of neighbouring habitats (monoculture oil palm, polyculture oil palm, housing, road, empty or unused land, grassland or low natural vegetation including ferns and cassava monoculture plantation), average density of nectar sources for butterflies (average of sums of density scales for all nectar source species from each plantation), average canopy openness, average percentage ground cover (bare ground, oil palm tree or sapling, other crops, cut frond, fern, other vegetation and other), average understorey vegetation height (from all sub-sample points), average oil palm height (average of all heights of the nearest oil palm trees to the four main sampling points within a plantation) and average epiphyte cover. Percentage leaf litter cover was removed from the analysis, because its values were directly implied by the other ground cover components. For the PCA, we used built-in R syntax, with a correlation matrix, and standardised all environmental data (due to differing units) using the function of 'SCALE = TRUE' in R. To create PCA biplots, we used 'factoextra' (Kassambara & Mundt, 2020). We ran ANOVA or Kruskal–Wallis tests (depending on the distribution and equality of variance of the principal component (PC) score data) to assess differences of the most influential PC scores between management types.

2.3.2 | Impacts of management decisions on butterfly assemblages

We checked for spatial autocorrelation among all plantations for butterfly assemblages using a Mantel test (Legendre et al., 2015) with 'vegan' package (Oksanen et al., 2020). To calculate the total species richness of butterfly assemblages in each of the plantations and across all plantations in each management type, we used the Chao1 index, which provides estimates of total species richness, accounting for the five plantations which were not surveyed completely (Gotelli & Colwell, 2011). Hence, rather than using the raw species richness data, we used estimates of species richness from the Chao1 index in subsequent analyses. To visualise the diversity of butterflies, we created species accumulation curves for all plots, separated by management decision type and separated by individual plantation, allowing us to account for unequal sampling effort in later analyses, related to incomplete surveys or sub-optimal conditions at the time of sampling. To create accumulation curves and calculate the Chao1 index, we used 'iNEXT' (Chao et al., 2014; Hsieh et al., 2020). Calculations and accumulation curves were created using abundance and species identity data, only including butterflies which were identified to species or morphospecies levels (Table S4).

We assessed whether alternative management decision types (mature monoculture, immature monoculture and immature polyculture) differed in the density and species richness of butterflies. The density used in the subsequent analyses was the density of butterflies per $500\,\mathrm{m}^2$, obtained by calculating the density of butterflies found per surveyed area over both days. Species richness data were estimates of species richness based on Chao1 index score per plantation. To assess any significant differences between management decision types, we ran separate Kruskal–Wallis tests (as data were not normal based on Shapiro–Wilk tests), with plantation type as the explanatory variable and density and species richness as outcome variables. We ran non-metric multidimensional scaling (NMDS) and produced stacked bar charts to visualise the assemblage composition of butterflies among management decisions. Finally, we ran an analysis of similarities (ANOSIM) to assess whether the composition of butterflies (only using butterflies identified to species or morphospecies level) differed between management decisions.

2.3.3 | Impacts of habitat structure and complexity on butterfly assemblages

To assess the direct impacts of habitat structure and complexity associated with management decisions on butterfly assemblages, we used generalised linear models (GLMs), with the most influential principal component (PC) scores (PC1–PC6), as a fixed factor (see Table S5). We chose to include 1–6 PC scores in our analyses, as each contributed >5% of environmental variation, and together explained the majority (63.1%) of the environmental variation. For all models, we multiplied PC3 and PC5 by −1, so scores were always in the direction of increasing complexity to aid interpretation. Species richness

and density were used in separate models as response variables. For GLMs run on each of the density and species richness of butterfly assemblages, we used a negative binomial family with log link, because of overdispersion. For both density and species richness analyses, we used log-likelihood ratio tests to assess the significance of each predictor, in which we compared full models with all predictors to models without one of the predictors. For GLMs run on the butterfly density, we ran sensitivity analyses by excluding sites (IM05, IP01, IP04, IP06, MM06 and MM08) that were influential in the original full model (points [oil palm sites] that fall at or beyond the Cook's distance on a Residual vs Leverage diagnostic plot). For sensitivity analyses, we multiplied PC6 by −1, so the direction of scores represented increasing complexity, to aid interpretation. We used 'lme4' (Bates et al., 2015) to run GLMs to assess the impacts of habitat structure and complexity (represented by summarised values of environmental parameters obtained from the PCA) on butterfly assemblages. We used 'MASS' (Venables & Ripley, 2002) to run negative binomial models. We used 'performance' (Lüdecke, Ben-Shachar, et al., 2021) to check overdispersion. All model assumptions were further checked using package 'see' (Lüdecke, Patil, et al., 2021), 'Rcpp' (Eddelbuettel, 2013; Eddelbuettel & Balamuta, 2018; Eddelbuettel & Romain, 2011) and 'patchwork' (Pedersen, 2023). We used 'vegan' (Oksanen et al., 2020) to run non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM).

3 | RESULTS

3.1 | Habitat structure and complexity across plantations

The first six PC scores explained most of the variation among environmental parameters, with PC1 and PC2 explaining 17.3% and 12% of variation, PC3 and PC4 explaining 9.6% and 9.2%, and PC5 and PC6 explain 8.5% and 6.6%, respectively (Table S5; Figure 1). Mature monoculture, immature monoculture and immature polyculture overlapped in terms of habitat structure and complexity, particularly for axes 2, 3, 4, 5 and 6 (Figure 1). However, environmental parameters explaining the structure and complexity of plantations differed significantly for PC1 (Table 1), with immature monoculture sitting in between mature monoculture and immature polyculture. Additionally, immature polyculture appeared much more variable. The average height, age and percentage epiphyte cover of oil palms all decreased from mature monoculture to immature monoculture and immature polyculture, while the percentage of cassava, banana and other crop types increased.

3.2 | Impacts of management decisions on butterfly assemblages

We recorded 1227 individual butterflies from 5 families (Nymphalidae, Papilionidae, Pieridae, Lycaenidae and Hesperiidae), 46 genera and 56

Management decision types [■] Mature monoculture [●] Immature monoculture [▲] Immature polyculture
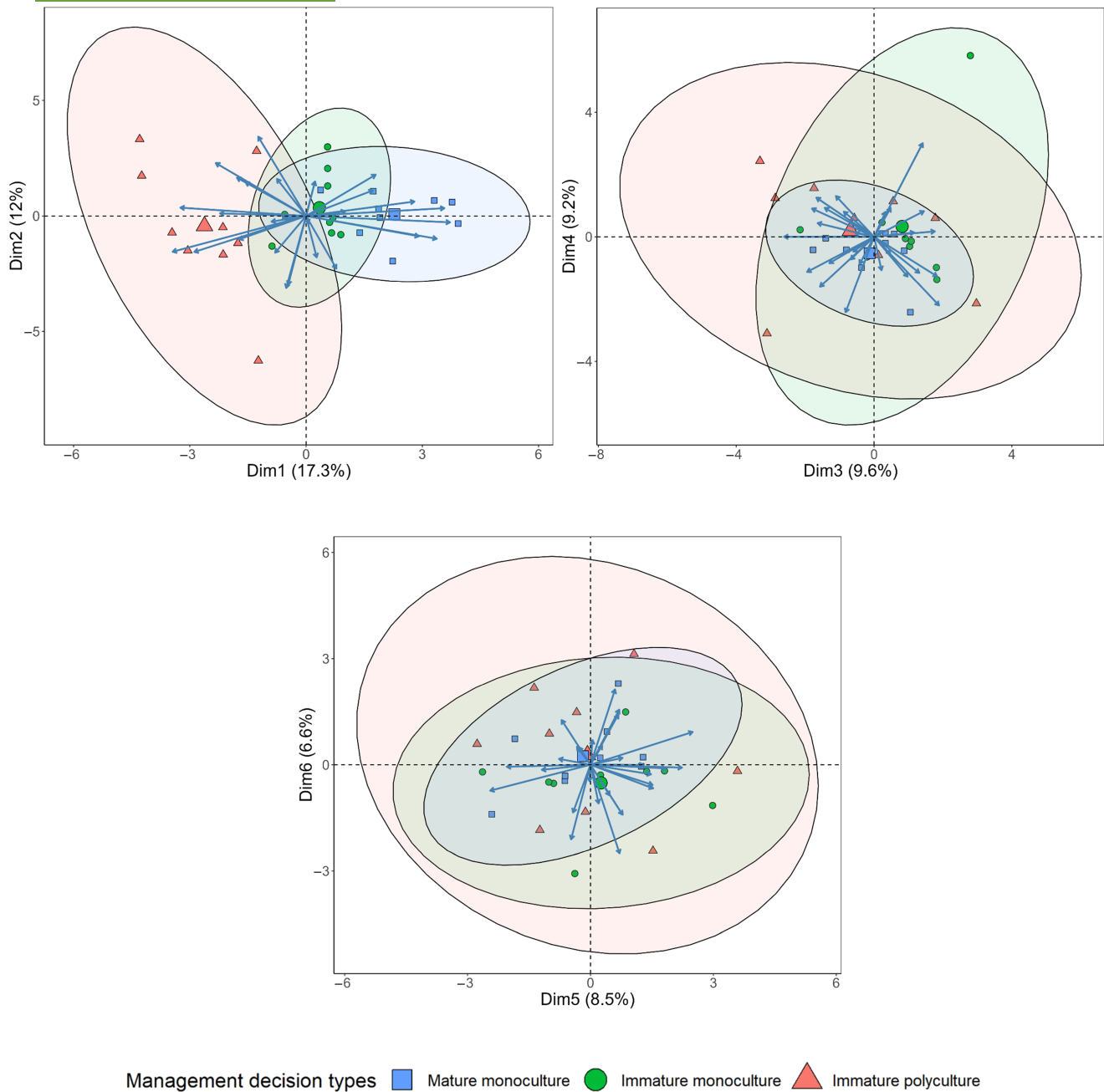
FIGURE 1 Principal component analysis (PCA) biplots showing PC1 and PC2 ('Dim1' and 'Dim2', top left panel), PC3 and PC4 ('Dim3' and 'Dim4', top right panel), and PC5 and PC6 ('Dim5' and 'Dim6', bottom panel) loading scores of plantations (coloured points) as well as environmental variables (arrows). Axes 1 and 2 explained 17.3% and 12% of the variation in environmental variables. Axes 3 and 4 explained 9.6% and 9.2%, respectively. Axes 5 and 6 explained 8.5% and 6.6%, respectively. In total, PC1–PC6 explained 63.2% of variation in the variables representing environmental conditions. This study used 27 plantations, consisting of nine of each of the management decision types (mature monoculture, immature monoculture and immature polyculture). Larger points represent the average values of management decision types, while smaller points represent individual plantations. Refer to Table S5 to see loadings of environmental variables assessed in the PCA.

species from all plantations surveyed (Table S4). The average density of butterflies per 500 m² was 13 (±4.87) in mature monoculture, 10.67 (±2.88) in immature monoculture and 18.44 (±6.65) in immature polyculture. The accumulation curves generated across plantation types seemed to reach an asymptote, indicating that sampling had recorded most of the species in our focal plantations. Using only

butterflies identified to species/morphospecies levels (946 individuals), mature monoculture had an estimated species richness (based on Chao1 index) of 42 (±5.43), immature polyculture 39 (±9.14) and immature monoculture 33 (±3.23) (Table 2; Figure 2). We found a significant but weak spatial autocorrelation among plantations for butterfly assemblages (Mantel test: $r=0.263$, p-value$=0.011$).

TABLE 1 Outputs of ANOVA or Kruskal–Wallis tests used to assess the difference in habitat structure and complexity between oil palm plantations across three differing management decisions (mature monoculture, immature monoculture and immature polyculture), consisting of nine plantations for each management decision type.

Compared PC scores	Group comparison	F/χ^2/diff[a]	p-value[b]
PC1	Overall	52.02	**<0.001*****
	Immature monoculture & immature polyculture	−2.966	**<0.001*****
	Immature monoculture & mature monoculture	1.935	**0.001****
	Immature polyculture & mature monoculture	4.901	**<0.001*****
PC2	Overall	0.680	0.711
PC3	Overall	1.925	0.168
PC4	Overall	2.395	0.301
PC5	Overall	0.176	0.840
PC6	Overall	0.888	0.425

Note: Habitat structure and complexity were represented by six PC scores (PC1–6) obtained from a PCA, which together explained 63.2% of environmental variability between management decision types. p-values that are less than 0.05 are given in bold and indicate significant differences.

[a]F-value if ANOVA, χ^2 if Kruskal–Wallis test, 'diff' in the case of post hoc analyses showing value differences between two compared groups.

[b]**, $0.001 < p\text{-value} < 0.01$; ***, $p\text{-value} < 0.001$.

TABLE 2 Outputs of Chao1 index calculations (shown as 'Estimator') used to estimate species richness across management decision types (mature monoculture, immature monoculture, immature polyculture; only butterflies identified to species/morphospecies levels were used).

Plantation type	Observed species richness	Estimator	Estimated standard error	95% lower confidence interval	95% upper confidence interval
Mature monoculture	42	49.17	5.43	43.92	68.84
Immature monoculture	33	35.99	3.23	33.53	49.77
Immature polyculture	39	50.96	9.14	42.17	84.18

Note: Observed species richness, standard errors of the calculations and confidence intervals are also shown.
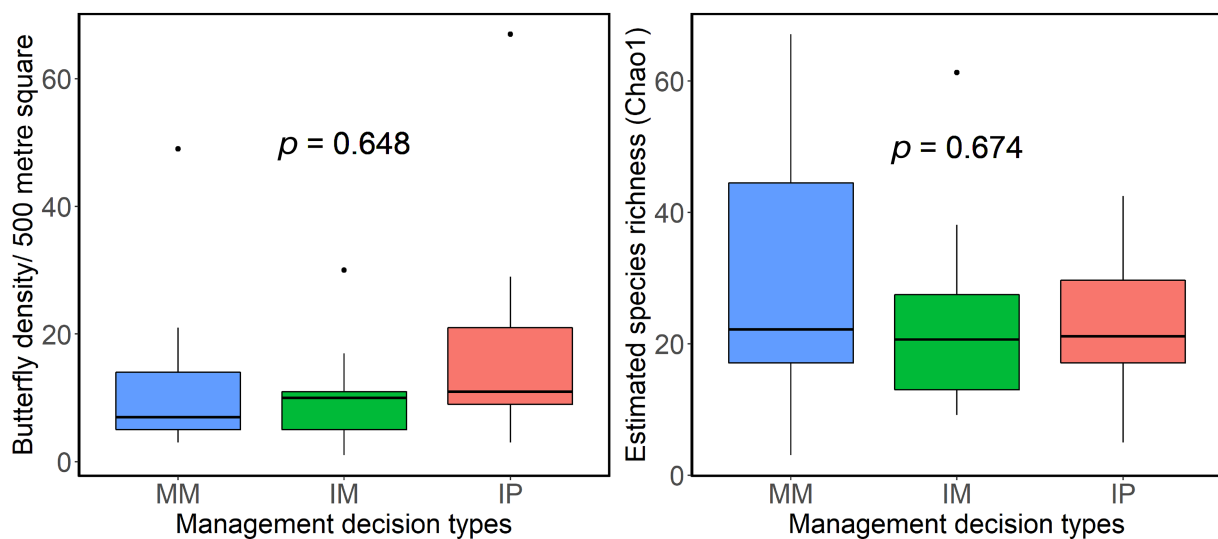
FIGURE 2 Effects of management decision types (IM, immature monoculture; IP, immature polyculture; MM, mature monoculture) on the density per 500 m^2 and estimated species richness of butterfly assemblages. p-values for both cases are >0.05, indicating non significant effects.

Of the 56 species/ morphospecies recorded, 49 were described as common species in Peninsular Malaysia (Corbet & Pendleburry, 2020) (Table S4). We found no endemic butterflies in this study. Across all plantations, *Amathusia phidippus* (Nymphalidae), *Appias libythea* (Pieridae), *Elymnias hypermnestra* (Nymphalidae), *Leptosia nina* (Pieridae), *Potanthus omaha* (Hesperiidae), *Ypthima baldus* (Nymphalidae) and *Ypthima huebneri* (Nymphalidae) were the most abundant (≥30 individuals), with *Elymnias hypermnestra* being found in the highest density (208 individuals across all plantations).

Although the species richness of butterflies varied substantially between individual plantations (Table S6; Figure S7), there were no significant differences in the density, estimated species richness (Table S7; Figure 2) or assemblage composition of butterflies between plantation types ($R = -0.034$, p-value $= 0.786$, Figure S8).

3.3 | Impacts of habitat structure and complexity on butterfly assemblages

Habitat structure and complexity significantly impacted the density, but not the species richness of butterflies (Table S8; Figure 3). In particular, PC2, PC3 and PC5 were significant predictors for butterfly density. Associated with PC2, butterfly density decreased with higher percentage of bare ground, percentage of polyculture plantation as a neighbouring habitat and plantation size, but increased with percentage of coconut and torch ginger in the plots, and the height of understorey vegetation (individual variables with highest loadings reported; see Table S5 for full details). Associated with PC3, butterfly density increased with percentage of monoculture plantation and road as neighbouring habitats, levels of nectar sources and percentage of other vegetation, but decreased with more housing and polyculture plantations as neighbouring habitat types, and cover of cut fronds (Table S5). Associated with PC5, butterfly density increased with higher percentage of road but lower percentage of oil palm monoculture as neighbouring habitat types, higher levels of nectar sources and yam, as well as lower percentage of fern and average height of understorey vegetation (Table S5). However, the observed trends were likely driven by a few outliers (IM05, IP01, IP04, IP06, MM06 and MM08). Removing the outliers, resulted in PC1, PC4 and PC6 being the only significant drivers for butterfly density (Table S9; Figure S9).

4 | DISCUSSION

4.1 | Habitat structure and complexity across plantations

Habitat structure and complexity generally overlapped across management types, with more variability in immature polyculture. However, there was a clear split across habitats for PC1, with average height of oil palm stands, age of oil palm and percentage epiphyte cover all increasing from immature polyculture to immature monoculture and mature monoculture, but average percentage of other crops, and percentage of cassava and banana decreasing. These differences are in line with the broad management decision types and demonstrate that replanting significantly affects the local environment, with immature monoculture generally appearing more similar to mature monoculture than immature polyculture. The trend also reflects the differences that occur as oil palm ages, with the height of oil palm increasing, epiphyte cover

going up and the canopy closing (Luskin & Potts, 2011), leading to a reduction in the cultivation of understorey crops. However, the high level of overlap suggests that differences in coarse habitat structure as a result of growing immature oil palm as a monoculture or polyculture, only have marginal effects on other aspects of habitat structure and complexity. It should be noted that this overlap may also be related to the characteristics of plantations surrounding our focal sites, which also influenced habitat characteristics. We acknowledge that the small size of individual plantations and the relatively small total study area of this project could limit the generalisability of our findings. However, the variability in management practices across smallholders and limited size of smallholder plantations is typical of systems of this kind (Comte et al., 2012; Razak et al., 2020), making our findings likely to be applicable to other related systems.

4.2 | Impacts of management decisions on butterfly assemblages

The total species richness we recorded was below the number of butterfly species recorded in related studies in forest, and only represented a small subset of all known species in Peninsular Malaysia: 56 in this study compared with 74 species in agroforestry orchards in Negeri Sembilan, Peninsular Malaysia (Wan Zaki et al., 2023), 138 species in forest in Pahang, Peninsular Malaysia (Suhaimi et al., 2017), and 1051 species recorded in the peninsula (Corbet & Pendleburry, 2020). However, this number was comparable to other studies conducted in oil palm, which recorded 54 species (Wan Zaki et al., 2023) and 20 species (Asmah et al., 2017) of butterflies, and 55 species of day-flying Lepidoptera (Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Ps, et al., 2023). Fifty out of 56 species we found were also common species, with larvae that feed on a range of plant species or have hostplants that were present in the study areas (Table S10, Corbet & Pendleburry, 2020). Therefore, although relatively diverse, the butterfly assemblage we found is dominated by disturbance-tolerant species, backing up findings from previous work (Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Ps, et al., 2023; Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Sudharto, et al., 2023). This highlights the importance of conserving forest habitats for butterfly diversity, especially those that are sensitive to environmental change.

There were no significant differences in the density (per $500\,m^2$), estimated species richness or composition of butterfly assemblages across management decision types. This finding might be related to overlap in environmental parameters between management types (Figure 1), or a greater importance of wider habitat characteristics in determining butterfly communities (Lucey & Hill, 2012), both of which could mean that butterflies
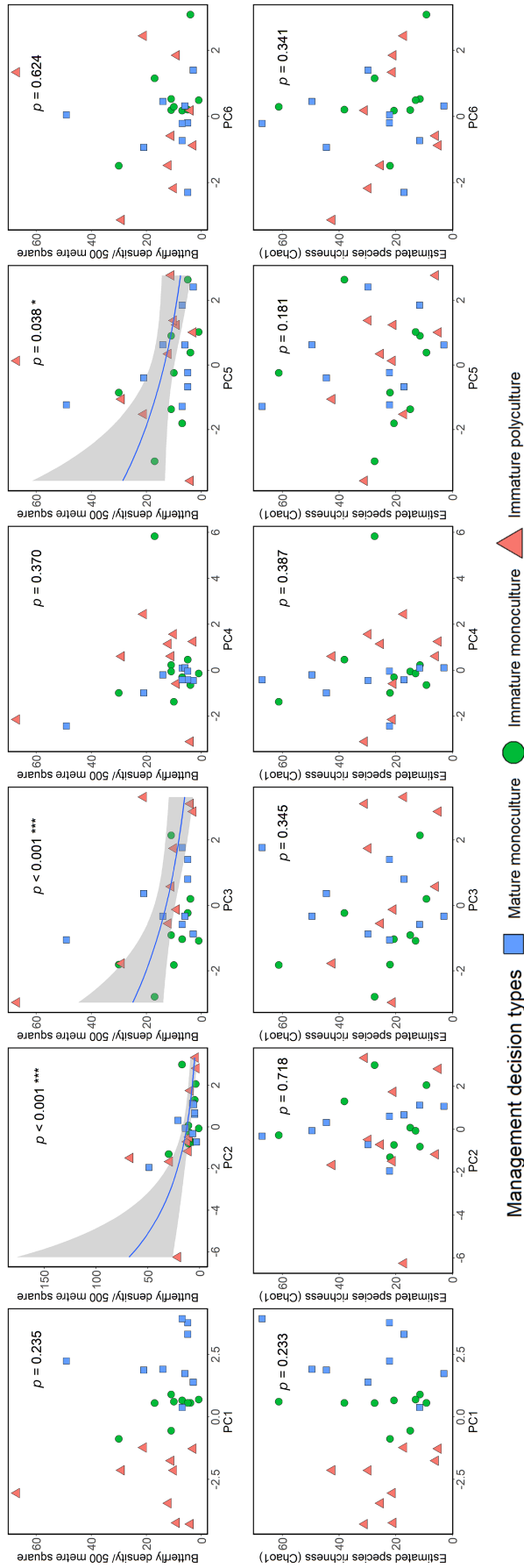
FIGURE 3 Effects of habitat structure and complexity associated with management decision types (mature monoculture, immature monoculture and immature polyculture), represented by PC1, PC2, PC3, PC4, PC5 and PC6 (obtained from PCA used to summarise environmental conditions) on the density and estimated species richness (based on Chao1 index) of butterfly assemblages. Trend lines generated from GLMs (generalised linear models) are shown for significant relationships. *p*-values from GLM are shown at the top right of each plot. Shaded areas represent 95% confidence intervals. PC3 and PC5 were multiplied by −1, so all trend lines are in the same directions (of increasing complexity) to aid visual comparison. Note for significant predictors: PC2 was mainly associated with higher percentage of bare ground, higher percentage of polyculture plantations as neighbouring habitat types, larger plantation size, but lower percentage cover of coconut and torch ginger, and lower height of understorey vegetation. PC3 was mainly associated with higher percentage of monoculture oil palm plantation and road, but lower percentage of housing, and polyculture plantations as neighbouring habitat types, as well as higher summed nectar sources for butterflies, higher percentage of other vegetation, but lower percentage of cut fronds as ground cover. PC5 was mainly associated with higher percentage of road but lower percentage of monoculture oil palm as neighbouring habitat types, higher summed nectar sources, and higher percentage of yam, as well as lower average percentage of fern as ground cover and lower average height of understorey vegetation. Finally, it should be noted that, when outliers were removed, significant predictors changed from PC2, PC3 and PC5 to PC1, PC4 and PC6 (please refer to Table S9 and Figure S9). *, 0.01 < *p*-value < 0.05; ***, *p*-value < 0.001.

did not differ greatly between plantation types. Indeed, we found that there was spatial autocorrelation in butterfly assemblages, indicating that wider landscape-scale patterns may have influenced results. As most species in our system were generalists and butterflies are dispersive, it could also be that the species we surveyed were robust to changes in management. This could also explain why we did not find differences in butterflies between mature and immature plantations, in contrast to Ashton-Butt et al. (2019), who found lower abundance and richness of soil macrofauna in replanted plantations, possibly reflecting the greater sensitivity and lower dispersal of soil taxa. Other studies in the region have also reported inconsistent differences between monoculture and polyculture plantations. For example, Ghazali et al. (2016) found a higher number of orders of arthropods from pitfall traps in polyculture plantations, but no significant differences in abundance or composition of arthropods. Azhar et al. (2014) found higher species richness of birds in monoculture oil palm than polyculture, but a higher abundance of birds in polyculture. A study conducted in oil palm plantations of mixed ages (between 2 and 30 years old [Asmah et al., 2017]) found that the species richness, abundance and composition of butterfly assemblages across monoculture and polyculture plantations did not differ significantly. These differing trends may reflect variable conditions across plantation types, or differing requirements across taxa, highlighting the need for more research. Accumulation curves also had overlapping error bars, indicating that differences in total species richness across management types were not substantial.

4.3 | Impacts of habitat structure and complexity on butterfly assemblages

Several environmental factors were significantly associated with the density of butterflies within plantations, although none had significant impacts on species richness. In particular, there was a higher density of butterflies (per 500 m^2) in smaller plantations, with lower percentage of bare ground and cut frond and fern cover, but higher percentage of other vegetation, as well as lower average height of understorey vegetation, higher percentage cover of coconut, torch ginger and yam, and higher levels of nectar sources for butterflies (Table S5). Additionally, neighbouring habitats were also a significant factor, with lower percentage of polyculture plantation and housing, but higher percentage of road being associated with higher densities of butterflies (Table S5).

These findings are likely to be related to resource availability (Lucey & Hill, 2012) and habitat condition. For example, smaller plantations could have a higher density of butterflies because available resources, such as hostplants and nectar sources, were concentrated in a smaller space. The higher density of butterflies with more understorey vegetation (Table S8; Wan Zaki et al., 2023) and higher level of nectar sources is likely to be because this habitat is used for perching, breeding and nectaring. The negative association with fern cover could be because ferns can become competitively

dominant in plantation understories, so their increased cover could reduce the diversity of other resources used by butterflies. Overall, these findings are in line with previous studies which found the importance of maintaining understorey vegetation within oil palm to maintain more diverse and abundant butterflies (Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Ps, et al., 2023; Reiss-Woolever, Advento, Aryawan, Caliman, Foster, Naim, Pujianto, Purnomo, Snaddon, Soeprapto, Tarigan, Wahyuningsih, Rambe, Sudharto, et al., 2023; Wan Zaki et al., 2023). The higher density of butterflies with a higher percentage cover of coconut (*Cocos nucifera*) and torch ginger (*Etlingera elatior*) could be because both these species are hostplants of butterfly species in this study. The presence and density of specific hostplants may have had a large influence on the number of individuals of each butterfly species recorded. Indeed, while we were not able to systematically survey hostplants and therefore include these in our analyses, we did note that a large number of these were present in our plots (Table S10).

Environmental conditions around a plantation are also likely to influence butterfly density, due to effects on resources and conditions. For example, the higher density of butterflies in plantations surrounded by less polyculture could be because polyculture provides favourable resources that draw butterflies out of the focal plantation (Table S5). Polyculture plantations and gardens in our study contained several kinds of crops and other plants which could be used by butterflies (Table S10). This interpretation is partially in contrast with the lack of difference we recorded between immature monoculture and polyculture plantations, but may be explained by the varying conditions across polyculture plantations, including the presence of hostplants in some, but not all. Finally, roads might have been a barrier to butterflies (Muñoz et al., 2015), again leading to relatively higher butterfly densities in the focal plantation.

Our sensitivity analyses showed some differences in terms of significant drivers for the density of butterflies. This variability suggests that results were influenced by outliers and indicates that further studies should be carried out. These inconsistencies could have been driven by the wide range of management decisions made by smallholders, resulting in the differing environmental conditions recorded within plantations affecting the density of butterflies (Table S9; Figure S9). For example, key factors associated with PC1, PC4 and PC6 comprised percentage coverage of other crops apart from oil palm as well as percentage bare ground and coverage of vegetation, reflecting varying management decisions composition between management by smallholders (Table S9).

4.4 | Management implications

We found few differences in habitat structure or butterfly species richness, density and composition between management decision types. Although this study was conducted at a local scale in fairly small plantation plots, this set-up is typical of smallholder landscapes of this type, and therefore likely to reflect findings across the region. Indeed,

similar results were also found by Asmah et al. (2017) who assessed fruit-feeding butterflies in immature oil palm mono- and polyculture and suggest that individual farmer management decisions have only limited impacts on butterflies. In contrast, we identified several environmental parameters that were associated with increases in butterfly abundance across plantations, although these findings were influenced by characteristics in a few key plantations (outliers in our analyses). Increasing the coverage of understorey vegetation, particularly of hostplants and nectar sources for butterflies, are likely to increase the abundance of butterflies and could potentially be implemented at little cost. Within a smallholder context, these approaches could be trialled by collectives of local communities, to boost the positive effects on butterflies across larger areas than single plantations.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data set (accompanied with analytic codes) are available at https://doi.org/10.5281/zenodo.10063971 (Harianja et al., 2023).

ORCID

Martina F. Harianja https://orcid.org/0000-0002-9607-6151
Jake Stone https://orcid.org/0000-0003-2151-4353
Sarah H. Luke https://orcid.org/0000-0002-8335-5960
Badrul Azhar https://orcid.org/0000-0003-0694-5294
Edgar C. Turner https://orcid.org/0000-0003-2715-2234

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Plantation size, oil palm age, as well as percentage of crops cultivated other than oil palm across plantations of differing management type used in this study.

Table S2: Percentage of neighbouring habitat types across plantations of differing management decisions in this study.

Table S3: Density of nectar sources (calculated using a scale of 1 to 5, based on Steffan-Dewenter and Tscharntke (1997)) across plantations of differing management decisions in this study.

Table S4: List of butterflies identified to species or morphospecies levels across all plantations in this study (946 out of 1227 butterflies surveyed in this study).

Table S5: Outputs of PCA (principal component analysis) used to summarise parameters representing environmental conditions across plantations with varying crop management (mature

monoculture, immature monoculture, and immature polyculture) in this study.

Table S6: Chao1 index scores ('Estimator') used to estimate species richness of butterfly assemblages across oil palm management types (only butterflies identified to species/morphospecies levels were used for calculations).

Table S7: Outputs of Kruskal–Wallis tests run to assess differences in the density (per $500\,m^2$) and estimated species richness of butterfly assemblages between the three plantation types.

Table S8: Outputs of log-likelihood ratio tests (X^2 and p-values) in GLMs (generalised linear models) run to assess the impacts of habitat structure and complexity associated with oil palm crop management (represented by PCA axes 1–6 [PC1, PC2, PC3, PC4, PC5, and PC6]) on the density (per $500\,m^2$) and estimated species richness (represented by Chao1 index) of butterfly assemblages across the 27 plantations (nine for each mature monoculture, immature monoculture, immature polyculture).

Table S9: Outputs of log-likelihood ratio tests (Deviance and p-values) in the GLMs (generalised linear models) run to assess the impacts of habitat structure and complexity associated with management decisions (represented by PC1, PC2, PC3, PC4, PC5, and PC6—PC3, PC5, and PC6 were multiplied by −1 before running the tests for visualisations) on the density (per $500\,m^2$) of butterfly assemblages across 18 plantations (out of 27 plantation plots in total)—*influential outliers that contributed most to the observed trend (replicates that fall at or beyond the Cook's distance on Residual vs. Leverage diagnostic plot) were removed* (IM05, IP01, IP04, IP06, MM06, and MM08). p-values that are less than 0.05 are given in bold and indicate significant impacts.

Table S10: List of butterflies surveyed in this study and their corresponding resources which were present in the study sites (except for ornamental cycad (Cycadaceae), the larval hostplant of *Chilades pandava*, which was found in a garden close to one of our study sites).

Figure S1: Study sites in Banting, Selangor, Peninsular Malaysia; comprising of nine smallholder-managed oil palm plantations of mature monoculture, immature monoculture, and immature polyculture.

Figure S2: Schematic illustrating a single study site and where perimeter (blue arrows) and central walks (black arrows) were conducted.

Figure S3: Schematic illustrating the set-up of measurements of environmental parameters within plantations done along the central line of each plantation.

Figure S4: $5\,m \times 5\,m$ sampling square for environmental parameter measurements within each plantation, created using two tape measures laid out in a cross shape with the central sample point at the centre of the cross.

Figure S5: Schematic to show the $5\,m \times 5\,m$ box that the person who was walking the transect imagined around them.

Figure S6: Accumulation curves based on abundance of butterfly assemblages found in two-day surveys for up to two-hour time window each day.

Figure S7: Accumulation curves of butterfly assemblages from mature monoculture (left), immature monoculture (middle), and mature polyculture (right) (plantations that consisted of fewer than 20 individuals were excluded for visualization: MM02, MM03, MM04, IM09, IP01, and IP03).

Figure S8: Effects of management decision types (MM = mature monoculture, IM = immature monoculture, IP = immature polyculture) on the composition of butterfly assemblages.

Figure S9: Effects of habitat structure and complexity associated with crop management (mature monoculture immature monoculture, and immature polyculture) represented by PC1, PC2, PC3, PC4, PC5, and PC6 (obtained from PCA used to summarise parameters representing environmental conditions) on the density of butterfly assemblages.