



Assessing the effects of oil palm replanting on arthropod biodiversity

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Abstract

1. Palm oil is the most traded vegetable oil worldwide. Production is concentrated in Southeast Asia, where established oil palm plantations dominate the landscape in many regions. Although levels of biodiversity are much lower than in forest, mature oil palm plantations can support a wide range of generalist species. However, these species may be threatened, as large areas of plantation have already been, or will soon be, replanted as they near the end of their productive life (20–30 years). Replanting changes vegetation complexity and microclimate, but short- and long-term effects on biodiversity are largely unstudied.
2. We surveyed an oil palm chronosequence (first-generation mature palms, and replanted second-generation palms aged 1, 3 and 8 years) in an industrial plantation in Riau, Indonesia to assess the impacts of replanting over an 8-year period on arthropods in the ground, understorey and canopy microhabitats. Replanting was carried out using current recommended strategies, which included staggering replanting events to promote landscape-level heterogeneity, retaining mature oil palm riparian buffers, planting a cover crop immediately after replanting, and using chopped mature palms as mulch after clearance. We assessed changes in total arthropod abundance and order-level community composition, as well as specific changes in spider communities.
3. We observed no significant declines in total arthropod abundance after replanting, but arthropod order-level community composition varied across the chronosequence in all microhabitats. These findings were replicated, or more pronounced, in spider-specific analyses. Spider abundance and species richness decreased in the understorey in the first year after replanting (although these returned to pre-replanting levels after 3 years), and spider species-level community composition in all microhabitats differed significantly across the chronosequence.
4. *Synthesis and applications.* Our findings indicate that total arthropod abundance is resilient to replanting of oil palm, but that replanting changes total arthropod and spider community composition and decreases spider abundance and species

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richness in some microhabitats. While it is somewhat encouraging from a management perspective that recommended replanting strategies maintain overall arthropod abundance, the changes in arthropod composition and spider biodiversity that we observed may impact ecosystem processes, such as pest control, in second-generation oil palm plantations, with potential implications for yield. Additional studies that focus on other taxonomic groups and assess the effects of individual replanting strategies are needed before the long-term ecological impacts of replanting on existing oil palm plantations can be fully determined.

KEYWORDS

arthropod, biodiversity, chronosequence, oil palm, replanting, spider, tropical agriculture

1 | INTRODUCTION

Palm oil—derived from oil palm fruits—is the most traded vegetable oil worldwide (>70 million metric tons traded in the 2019/2020 fiscal year; USDA, 2020), and oil palms are the most productive vegetable oil crop (5.5 tonnes/ha oil output; Zimmer, 2010). Oil palms grow on 21.3 million hectares across the tropics (FAO, 2019), with production led by Indonesia and Malaysia, which together account for 84.7% of global supply (USDA, 2020). Here, oil palm plantations have often replaced natural habitat (e.g. Koh, Miettinen, Liew, & Ghazoul, 2011; Sodhi, Koh, Brook, & Ng, 2004; Vijay, Pimm, Jenkins, & Smith, 2016). Converting forests to oil palm reduces biodiversity across a wide range of taxa (Barnes et al., 2017; Drescher et al., 2016; Edwards et al., 2014; Fitzherbert et al., 2008; Foster et al., 2011; Savilaakso et al., 2014) and causes changes in ecosystem functions, including soil fertility and water quality (Dislich et al., 2017).

Retaining natural habitats is paramount to mitigating biodiversity losses (Gibson et al., 2011), but steps should also be taken to improve biodiversity within existing oil palm plantations (Luke, Advento, Aryawan, et al., 2020). Managing for biodiversity in plantations is important to both conservation and profitability, owing to the essential ecosystem services that many taxa provide (Dislich et al., 2017; Foster et al., 2011). Oil palm plantations have the potential to support more biodiversity than many other crops—particularly annuals such as rice—owing to their 20- to 30-year commercial life cycle (Corley & Tinker, 2016; Meijaard et al., 2018; USDA, 2012). Oil palms reach peak production after 6–10 years and, after this time, plantations can develop stable microclimates (Luskin & Potts, 2011), structurally complex vegetation (Luke et al., 2019), and increased soil organic carbon (Pauli et al., 2014), increasing habitat stability and providing resources for biodiversity. For instance, mature oil palm plantations have been found to support abundant and relatively diverse communities of plants (Luke et al., 2019), fungi (Brinkmann et al., 2019), birds (Azhar et al., 2011), dragonflies (Luke, Advento, Dow, et al., 2020) and mammals (Pardo et al., 2019), among other taxonomic groups.

Terrestrial arthropods are some of the most diverse and functionally important taxa within oil palm plantations. They facilitate

a wide range of ecosystem functions (Dislich et al., 2017), which include reducing pest activity (Turner & Hinsch, 2017), recycling waste (Gray, Slade, Mann, & Lewis, 2014) and pollinating oil palm inflorescences (Li, Tschardtke, Saintes, Buchori, & Grass, 2019; Vaknin, 2012). However, arthropods can also be oil palm pests, causing ecological and economic damage (Corley & Tinker, 2016; Dislich et al., 2017). Changes to routine plantation management, for instance intercropping with other crops (Ashraf et al., 2018; Ghazali et al., 2016) or enhancing understorey vegetation complexity (Ashton-Butt et al., 2018; Spear et al., 2018), have the potential to increase arthropod abundance and diversity. Employing management strategies that boost populations of beneficial arthropods, such as predatory spiders, while suppressing pests can lead to more productive, as well as more biodiverse, oil palm systems (Turner & Hinsch, 2017).

The relatively high levels of biodiversity that can develop within oil palm plantations are potentially threatened by replanting (Ashton-Butt et al., 2019; Snaddon, Willis, & Macdonald, 2013). Oil palms are replanted once they pass peak yields, at around 20–30 years old (Corley & Tinker, 2016). The process of replanting mature plantations with young palms is highly destructive and results in substantial soil disturbance, vegetation loss, and a much hotter and drier microclimate (Ashton-Butt et al., 2019; Kurz et al., 2016; Snaddon et al., 2013). Across Southeast Asia, large swathes of first-generation mature oil palms (i.e. palms that replaced forest during large-scale oil palm expansion in the 1990s) have already been replanted, or are likely to be replanted in the near future, presenting a novel phase for the palm oil industry.

Despite the substantial environmental changes that occur as oil palm is replanted, we know of only four published studies that have examined the effects of replanting on oil palm biodiversity and functions, and these have found no consistent ecosystem responses (Ashton-Butt et al., 2019; Kurz et al., 2016; Waters, 2018; Woodham et al., 2019). Furthermore, these studies focus on only one microhabitat (Ashton-Butt et al., 2019; Kurz et al., 2016; Waters, 2018), or taxonomic group (Kurz et al., 2016; Waters, 2018). Therefore, there is still substantial uncertainty about the short- and long-term impacts of replanting on oil palm

ecosystems. This has led stakeholders to identify the development of sustainable replanting strategies as a top priority for oil palm research (Padfield et al., 2019). Current recommended strategies that may benefit oil palm ecosystems include staggering replanting events within large-scale plantations to promote landscape-level heterogeneity (Luskin & Potts, 2011), retaining riparian buffers (Barclay et al., 2017), planting a cover crop immediately (<2 months) after replanting to protect soil (Corley & Tinker, 2016), and using chopped palm trunks as mulch in second-generation plantations (Corley & Tinker, 2016).

This study investigates the effects of oil palm replanting on terrestrial arthropods in industrial plantations in Riau, Indonesia. We sampled a chronosequence of first-generation mature oil palm, and second-generation oil palms aged 1, 3 and 8 years, which had been replanted using recommended replanting strategies. We quantified the environmental conditions and arthropod community (all arthropods identified to order level and spiders to family and morphospecies level) in ground, understorey and canopy microhabitats to answer the following questions: (a) How does microclimate and vegetation complexity change after replanting? (b) Does within-microhabitat total arthropod abundance and order-level community composition change after replanting? We then conducted focussed analyses on spiders—a key predatory group within oil palm—to investigate whether order-level trends were replicated at higher taxonomic resolution, asking (c) Does within-microhabitat spider abundance, species richness and morphospecies-level community composition change after replanting?

2 | MATERIALS AND METHODS

2.1 | Site

Fieldwork was based in industrial oil palm plantations in Riau, Sumatra, Indonesia (N0 55.559, E101 11.619; Figure 1). The plantations are owned by PT Ivo Mas Tunggal (a subsidiary company of Golden Agri Resources [GAR]), and run with management advice from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI), the research and development centre of GAR. Historically, the region was lowland rainforest but, after logging in the 1970s, it was converted to oil palm monoculture (1985–1995). The closest forest network (>5,000 ha) is now nearly 30 km away. The area is composed of seven oil palm estates, which are split into divisions and further divided into 300 × 1,000 m blocks, intersected with roads. Estates are managed following standard industry practices (see Table S1; Luke, Advento, Aryawan, et al., 2020 for more details) and in line with Roundtable on Sustainable Palm Oil (RSPO; <http://rspo.org>), Indonesian Sustainable Palm Oil (ISPO; <http://ispo.org.or.id>) and International Sustainability & Carbon Certification (ISCC; <http://iscc-system.org>) guidelines. Regional temperature is an average of 26.8°C and mean annual rainfall is 2,350 mm (see Tao, Slade, Willis, Caliman, & Snaddon, 2016). Climate and rainfall are influenced by the El Niño Southern Oscillation (see Eycott et al., 2019).

Replanting of first-generation oil palms across the estates began in 2010, in areas that were identified as being more than 25 years old, having fewer than 100 palms/ha, and yielding less than 14 tonnes of oil/ha each year. Replanting occurred using a suite of recommended replanting strategies (Figure S1). These included retaining mature oil palm riparian buffers (50 m in width on both sides of the river; Barclay et al., 2017), planting a leguminous cover crop (primarily *Mucuna bracteata* but also *Pueraria javanica* and *Calopogonium mucuoides*) immediately (<2 months) after clearance of mature palms to maintain soil health (Corley & Tinker, 2016), and using large diggers to uproot and then chop mature palms, which were later used as mulch (Corley & Tinker, 2016). SMARTRI has also staggered replanting events in approximate 1-yearly intervals (each estate replants no more than 4% of its planted area each year and ensures that immature palms, which cannot be harvested, are never more than 12% of its total planted area) to increase landscape-level heterogeneity across the plantation (Luskin & Potts, 2011). Over time, this has resulted in a landscape mosaic of differently aged oil palm.

We established study sites across this chronosequence in four age cohorts (hereafter, 'cohorts') in a space-for-time design, to investigate the impacts of replanting over an 8-year post-replanting period (Figure 1). We chose cohorts that differed from each other environmentally and were of industry importance (Figure S1):

- First-generation mature palms (31–33 years old; 'Age M'). These palms were established on previously forested land. Palms were still being harvested but were past peak yields and had closed canopies and a well-developed understorey of shade-tolerant plants, particularly ferns (mostly *Nephrolepis biserrata*, *Asplenium longissimum* and *Dicranopteris linearis*). Understorey vegetation along access paths and within a 1.5 m radius of palm trunks was cleared using herbicide to facilitate access. Palms were ~15- to 18-m tall.
- Second-generation 1-year-old palms ('Age 1'). These palms were before yielding age, had open canopies and were surrounded by leguminous cover crop. Palms were ~2 m tall.
- Second-generation 3-year-old palms ('Age 3'). These palms had just reached yielding age, and harvesting paths (~3 m wide) had been made between every other row of palms in areas that were not on steep slopes or prone to flooding. Herbicides were used to clear understorey vegetation around palm trunks. Canopies were more extensive than those in Age 1 but remained open. Palms were surrounded by leguminous cover crop and were ~4 m tall.
- Second-generation 8-year-old palms ('Age 8'). These palms had reached fruiting maturity and had closed canopies. Shade-tolerant understorey plants had replaced the leguminous cover crop. Heavy equipment used for harvesting had flattened or cleared some vegetation between palms, and vegetation was cleared manually around palm trunks. Palms were ~7 m tall.

We established four study sites in each cohort and split sites within a cohort across two estates (except in Age 8, where

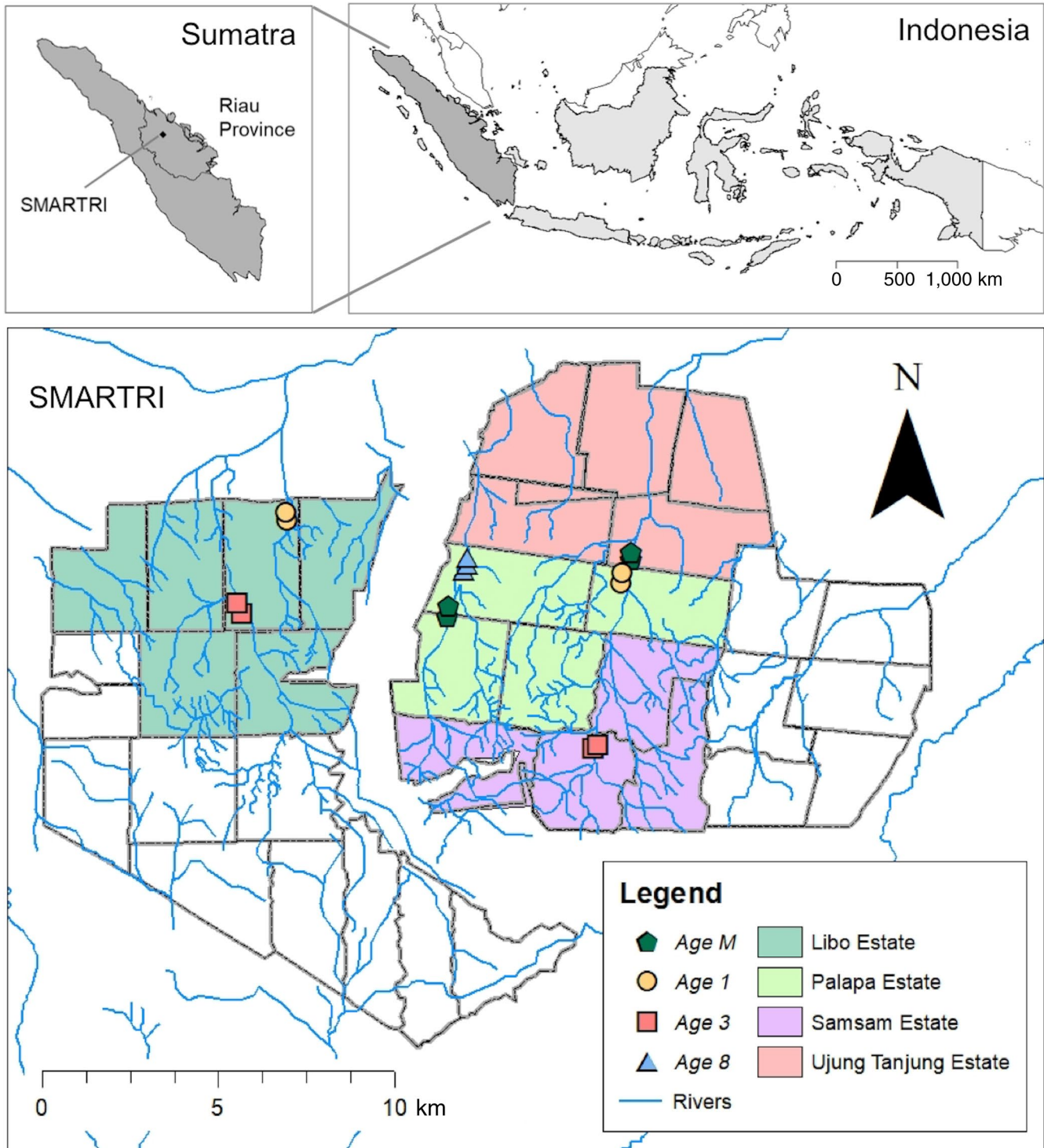


FIGURE 1 Maps showing the location of study sites (Riau, Sumatra, Indonesia). Estates used in this study (Libo, Palapa, Samsam and Ujung Tanjung) are shown in colour. Study sites in Ages M, 1, 3 and 8 are represented, respectively, by pentagons, circles, squares and triangles. At each site, we established a 100 m transect with sampling points at the start, middle and end. Due to spatial constraints, two Age 1 transects were within 100 m of each other, and two Age 8 transects were only 135 m apart. All other transects were at least 300 m apart. All sites were 125 m from riparian buffers, consisting of 50-m wide areas of mature palm on each riverbank. We made maps using ArcMap 10.5.1 (Environmental Systems Research Institute (ESRI), 2017), and package MAPS (Brownrigg, 2018), with reference to maps supplied by SMARTRI

availability only allowed three sites within one estate; Figure 1). We interviewed estate managers to ensure that management was broadly consistent across sites within a cohort (Table S1). At each of

the 15 sites, we established a 100 m transect with three independent sampling points, each located 50 m apart. Due to spatial constraints, two Age 1 transects were within 100 m of each other, and

two Age 8 transects were only 135 m apart, but all other transects were at least 300 m apart. All transects were 125 m from retained riparian buffers.

2.2 | Data collection

2.2.1 | Environmental conditions

Data collection occurred from February to May 2018, during the regional rainy season. We measured environmental conditions along 12 transects ($n_{Age\ M} = 2$, $n_{Age\ 1} = 3$, $n_{Age\ 3} = 4$, $n_{Age\ 8} = 3$) to characterize changes in vegetation complexity and microclimate across the chronosequence. We measured understorey vegetation height, understorey vegetation composition and canopy openness at 10-m intervals along transects (11 data points per transect; Vegetation and Canopy: $n_{Age\ M} = 22$, $n_{Age\ 1} = 33$, $n_{Age\ 3} = 44$, $n_{Age\ 8} = 33$). We measured vegetation height using a drop disc (30 cm diameter and 231 g, dropped from an initial height of 170 cm), as similar methods have previously proven successful for measuring vegetation height in oil palm (Luke et al., 2019). We classified the dominant understorey vegetation type(s) touching the disc into four categories: fallen oil palm frond, herbaceous plant, bare ground and fern. We measured canopy openness using a spherical densiometer (Lemmon, 1956), alternating facing left and right as we measured along each transect. We also measured soil temperature using iButton dataloggers (DS1922L-F5 thermochrons at high capacity). We set dataloggers to record for 24 hr at 3-hourly intervals, placing them in mesh bags that were buried 5 cm below the soil surface at the first sampling point in each transect. Each datalogger recorded eight temporal data points. One datalogger in Age 3 overheated, and therefore no soil temperatures were obtained at this transect (Temperature: $n_{Age\ M} = 16$, $n_{Age\ 1} = 24$, $n_{Age\ 3} = 24$, $n_{Age\ 8} = 24$).

2.2.2 | Order-level arthropod sampling

We sampled arthropods across all 15 transects in three microhabitats: ground, understorey and canopy. To sample ground arthropods, we placed a single pitfall trap (19.5 cm diameter at mouth) at each sampling point. Pitfall traps were partially filled with 70% ethanol and covered with a plastic plate to prevent rainfall dilution and flooding. To sample understorey arthropods, we placed a brown sticky trap (sticky on both sides, with a total sticky area of 19 cm × 27 cm) adjacent to each pitfall trap, and hung approximately 1.5 m from the ground using string. All traps along a transect were set on the same day. We collected both pitfall and sticky traps after 72 hr (Ground and understorey arthropods: $n_{Age\ M} = 12$, $n_{Age\ 1} = 12$, $n_{Age\ 3} = 12$, $n_{Age\ 8} = 9$).

After pitfall and sticky traps were collected, we sampled canopy arthropods using insecticide fogging. To fog, we suspended six trays (each 1 m in diameter) under a single focal palm at the start of each transect and tessellated trays such that half were flush against the trunk and half were under the canopy. Although the distance

between trays and canopies varied between cohorts, we kept fogging methods constant so that samples from all cohorts were comparable and each represented a consistent area of vertical space sampled per palm. We fogged each focal palm (Canopy arthropods: $n_{Age\ M} = 4$, $n_{Age\ 1} = 4$, $n_{Age\ 3} = 4$, $n_{Age\ 8} = 3$) using a Pulsfog K-10-SP Portable Thermal Fogger filled with a solution of 4.950 L diesel and 50 ml insecticide (Matador 25 EC, 25 g/L lambda-cyhalothrin). We fogged for 60 s after making sure that the fog had completely enveloped the oil palm canopy, as it was previously shown that similar fogging times collected large numbers of arthropods in oil palm plantations (Turner & Foster, 2009), and we sought to limit the impact on the wider environment. We collected arthropods from trays after 2 hr. All fogging was completed before 09:45 and during periods of minimal wind and no rain.

We identified all arthropods using stereomicroscopes in laboratories at SMARTRI research centre. We identified most arthropods to order-level, although we identified Chilopoda and Diplopoda to class and separated Formicidae (family) and Isoptera (infraorder) to their own groups, owing to their distinctive ecology and to be consistent with a comparable previous study (Ashton-Butt et al., 2019). We also placed endopterygote larvae in their own group. Hereafter, we collectively refer to all groups as orders. Identifying to order-level allowed all samples to be identified with the resources available and provided an overview of the responses of the total arthropod community to replanting.

2.2.3 | Species-level spider sampling

We conducted focussed analyses on spiders in all microhabitats, to determine whether arthropod-level trends were replicated when taxonomic resolution was increased. We focussed on spiders, in part due to their contributions to pest control in croplands (Michalko, Pekár, Dul'a, & Entling, 2019) and also because adults could be reliably identified to morphospecies. We collected ground and canopy spiders during pitfall trapping and canopy fogging, as described above (Ground spiders: $n_{Age\ M} = 12$, $n_{Age\ 1} = 12$, $n_{Age\ 3} = 12$, $n_{Age\ 8} = 9$; Canopy spiders: $n_{Age\ M} = 4$, $n_{Age\ 1} = 4$, $n_{Age\ 3} = 4$, $n_{Age\ 8} = 3$). Understorey spiders caught on sticky traps were often partially damaged and difficult to identify. We, therefore, collected understorey spiders by walking each transect and collecting all spiders located above the ground and within 1 m of the observer (Understorey spiders: $n_{Age\ M} = 4$, $n_{Age\ 1} = 4$, $n_{Age\ 3} = 4$, $n_{Age\ 8} = 3$). We walked all transects during the day between 07:00 and 14:00 and when it was not raining. In the laboratory, we separated juveniles from adults (dissecting when necessary to differentiate haplogyne adult females and juveniles), and identified adults to family and morphospecies (hereafter, 'species') using dissecting microscopes and relevant keys (<http://ecotaxonomy.org/ecokeys>; Deeleman-Reinhold, 2000; Jocqué & Dippenaar-Schoeman, 2006). It was not possible to match males and females for all species, and therefore we counted each unique male and female as its own species. The spiders are preserved in 75% ethanol at SMARTRI research centre.

2.3 | Statistical analyses

All statistical analyses were performed in R version 3.5.1 (R Core Team, 2018) within R Studio version 1.1.456 (R Studio Team, 2018). We used *readxl* (Wickham et al., 2019), *tidyverse* (Wickham, 2017), *zoo* (Zeileis, Grothendieck, Ryan, & Ulrich, 2019), *data.table* (Dowle et al., 2019), *plyr* (Wickham, 2016), *ggsignif* (Ahmann-Eltze, 2019), *lemon* (Edwards, Auguie, Jackman, Wickham, & Chang, 2019), *car* (Fox et al., 2020) and *cowplot* (Wilke, 2019) for data wrangling, exploration and visualization. Exploration followed Zuur, Ieno, and Elphick (2010). We fitted generalized additive models (GAMs) using *mgcv* (Wood, 2019), generalized linear models (GLMs) using MASS (Ripley et al., 2019), generalized linear mixed models (GLMMs) using *glmmTMB* (Magnusson et al., 2019), Kruskal–Wallis tests using *stats* (R Core Team, 2018) and multivariate generalized linear models (mGLMs) using *mvabund* (Wang et al., 2019).

Unless otherwise stated, we fitted models to negative binomial distributions using log links, included cohort as a fixed effect (levels: *Age M*, *Age 1*, *Age 3*, *Age 8*) and, for mixed models, Transect ID as a random intercept effect. We validated models by plotting Pearson residuals against fitted values and covariates and verifying no patterns were present. To ensure our models fitted the observed data, we simulated 10,000 datasets from each model, calculated dispersion statistics for each simulated dataset, and verified that the dispersion statistic from our model was within the range of dispersion statistics calculated from our simulations (Zuur & Ieno, 2016). Our simulations indicated that there were no issues in model fit. We determined the significance of cohort to each model by comparing fitted models with null models using likelihood ratio tests (LRTs). If mixed models suggested a moderately significant effect of cohort ($0.01 < p < 0.07$), we re-calculated p values based on parametric bootstrapping using *DHARMa* (Bates, Mächler, Bolker, & Walker, 2015; Hartig, 2019). If cohort was confirmed to be significant, we used *multcomp* (Hothorn et al., 2019) to conduct post-hoc analyses (Tukey all-pair comparisons, adjusting p values using the Bonferroni correction) to identify cohorts between which significant differences occurred.

2.3.1 | Impacts of replanting on the environment

We analysed vegetation height and canopy openness using GLMMs, to account for non-independence of measurements along the same transect. We fitted the canopy openness GLMM to a normal distribution (identity link), after applying a logit transformation to the data to meet model assumptions (Warton & Hui, 2011). During data exploration, we noticed *Age 3* had high variability in canopy openness, owing to several data points that were collected near palm trunks (i.e. areas with unusually low canopy openness, in comparison to the majority of the *Age 3* landscape). We therefore eliminated *Age 3* data that were more than one standard deviation away from the mean ($n_{\text{eliminated}} = 9$ data points) and, as a sensitivity analysis, re-ran our model on the adjusted dataset to explore the impact of the eliminated *Age 3* data on our initial model findings. We described

understorey vegetation composition along transects using stacked bar charts that conveyed percent vegetation occurrence by vegetation category. We analysed soil temperature using a GAM fitted to a Gaussian distribution (identity link). We fitted a smoothing function (using cyclic penalized cubic regression splines and multiplied by the fixed effect) to the time of day at which recording occurred, and used an F -test to determine the significance of cohort.

2.3.2 | Impacts of replanting on all arthropods

We analysed total arthropod abundances separately for the ground, understorey and canopy microhabitats. Prior to analysing understorey data, we eliminated ant abundance from one sample due to an extremely high abundance of winged ants that had emerged from one nest and flown into the trap. When fogging, five sample trays across two palms overturned before collection and so samples were lost. We therefore standardized abundance data for each palm prior to analysis by calculating mean abundance per tray and multiplying by 6 (the number of trays set per palm). We also rounded to the nearest integer to meet model assumptions. We analysed ground and understorey abundances using GLMMs, to account for non-independence of traps along the same transect. We analysed canopy abundances using a GLM, but model validation indicated patterns in the residuals. For this reason, and due to the small sample size, we re-analysed these data using a Kruskal–Wallis test.

We used mGLMs (Warton & Hui, 2017; Warton, Wright, & Wang, 2012) to analyse arthropod order-level community composition. In these analyses, we excluded endopterygote larvae and individuals that could not be identified to order. After removals, 97.2% of all collected arthropods still remained and were used in analyses. We validated mGLMs by plotting Dunn–Smyth residuals against fitted values and covariate cohort (Wang et al., 2019; Wang, Naumann, Wright, & Warton, 2012). We determined a significant effect of cohort using LRTs and by bootstrapping probability integral transform (PIT) residuals using 10,000 resampling iterations (Warton, Thibaut, & Wang, 2017). We included Transect ID as a blocking variable when calculating p values in our ground and understorey analyses, to account for non-independence of traps along the same transect. If cohort was significant ($p < 0.05$), we ran univariate analyses on individual arthropod orders. We adjusted univariate p values to correct for multiple testing using a step-down resampling algorithm (Wang et al., 2012), but otherwise our statistical approach remained unchanged from the multivariate parent models.

2.3.3 | Impacts of replanting on spiders

To better understand the spider assemblage within the plantation, and to assess our sampling completeness, we calculated interpolated and extrapolated species richness, based on adult data only, within each microhabitat (using the richness estimators derived by Chao et al., 2014 and *iNEXT* (Hsieh, Ma, & Chao, 2016, 2019)) and plotted

these as species accumulation curves. We extrapolated to double the number of observed individuals. We separately analysed spider abundance and species richness for the ground, understorey and canopy microhabitats. We used all collected spiders in abundance analyses, but we only included adults in species richness analyses. We analysed ground spider abundance and species richness using GLMMs, to account for non-independence of traps along the same transect. We analysed understorey and canopy spider abundance and species richness using GLMs but, due to patterns in residual plots and our small sample size, we re-analysed these data using Kruskal–Wallis tests. When cohort was significant, we used *dunn.test* (Dinno, 2017) to conduct post-hoc analyses (Dunn's Test for Multiple Comparisons, adjusting p values using the Bonferroni correction). We used mGLMs to analyse spider species-level community composition, based on adults only. We included Transect ID as a blocking variable when calculating p values in our ground analysis, to account for non-independence of traps along the same transect. If cohort was significant ($p < 0.05$), we ran univariate analyses on individual spider species. Our statistical approach otherwise remained unchanged from our arthropod order-level community composition analyses.

3 | RESULTS

3.1 | Impacts of replanting on the environment

Replanting affected vegetation composition, canopy openness (Canopy openness: LRT = 43.015, $p < 0.001$ [sensitivity analysis: LRT = 63.628, $p < 0.001$]; Table S2) and soil temperature (soil temperature: $F = 18.100$, $p < 0.001$; Table S2), but not vegetation height (vegetation height: LRT = 5.199, $p = 0.158$; Table S2; Figure 2a). Compared to Age *M*, vegetation composition in Ages 1 and 3 had higher densities of herbaceous plants and lower densities of ferns (Figure 2b). Vegetation composition in Ages *M* and 8 was similar, although more fallen palm fronds and bare ground were present in the latter. Canopy openness in Ages 1 and 3 was greater than in Ages *M* and 8 ($p < 0.001$ for all). Age 1 had a more open canopy than Age 3 ($p = 0.004$), although this difference was dependent on the nine extreme values in Age 3, as our sensitivity analysis indicated no difference in openness between these cohorts ($p = 0.334$). This indicated that, away from palm trunks (i.e. the majority of the Age 3 landscape), openness in Ages 1 and 3 was not different. Openness was not different between Ages *M* and 8 ($p = 0.417$; Figure 2c), although this lack of difference was dependent on the nine extreme values in Age 3. After eliminating these Age 3 values in our sensitivity analysis, the standard errors around all model estimates shrunk, leading to our post-hoc comparisons indicating that Age 8 had a more closed canopy than Age *M* ($p < 0.001$; Table S3). Soils in Age 1 were hotter than in Age *M* ($p = 0.002$), Age 3 ($p < 0.001$) and Age 8 ($p < 0.001$). Soils in Age 8 were cooler than in Age 3 ($p = 0.009$) and Age *M* ($p = 0.030$; Figure 2d; Table S4). Temperature varied across the day in all cohorts ($p < 0.002$ for all), but the degree of variability was not the same.

Cross-day variability in Age 1 (25.3–32.4°C) and Age 3 (24.3–30.7°C) was approximately double that in Age *M* (25.6–28.9°C) and Age 8 (24.9–27.8°C). This was also indicated by the smoothing functions for Ages 1 and 3 being more non-linear than those for Ages *M* and 8 (Figure S2).

3.2 | Impacts of replanting on all arthropods

We collected 15,854 arthropods, of which 7,955 were from pitfall traps, 4,736 were from sticky traps and 3,163 were from canopy fogging (after correcting for overturned fogging trays). Replanting did not affect ground arthropod abundance (Ground arthropod abundance: LRT = 3.317, $p = 0.345$; Figure 3a-Left; Table S5), although abundance was highly variable in Age *M* (owing to large variation in numbers of Collembola and—to a lesser extent—Araneae and Coleoptera) and less variable in Age 8 compared to other cohorts. Understorey arthropod abundance increased in the first year after replanting (Age *M* to Age 1) but returned to pre-replanting levels by Age 3. The conditional model suggested cohort was a significant predictor of this effect (Understorey arthropod abundance: LRT = 9.024, $p = 0.029$); however, parametric bootstrapping indicated that the effect was not significant (Understorey arthropod abundance: $p_{10000 \text{ iter}} = 0.077$; Figure 3a-Centre; Table S5). Similarly, canopy arthropod abundance did not differ after replanting (Canopy arthropod abundance: $\chi^2 = 5.392$; $p = 0.145$; Figure 3a-Right; Table S5), but abundance in Age 8 was highly variable (owing to large variation in numbers of Acari, Araneae, Collembola, Diptera and Formicidae), with one palm having more than triple the arthropod abundance of any other palm.

We identified 15,596 of the 15,854 arthropods (98.4%) to 24 orders, including 7,955 from pitfall traps (100%; Table S6), 4,479 from sticky traps (94.6%; Table S7) and 3,162 from canopy fogging (99.9%; Table S8). The majority of non-identifiable arthropods were damaged individuals. Of the identified arthropods, 15,405 were used in order-level community composition analyses, including 7,916 from pitfall traps, 4,479 from sticky traps and 3,010 from canopy fogging. Collembola ($n = 3,649$), Formicidae ($n = 2,191$) and Coleoptera ($n = 751$) were dominant on the ground; Diptera ($n = 2,727$), Hemiptera ($n = 432$) and Coleoptera ($n = 360$) were dominant in the understorey; and Araneae ($n = 456$), Acari ($n = 388$) and Diptera ($n = 379$) were dominant in the canopy. Ground (LRT = 186.1, $p = 0.013$), understorey (LRT = 177.0, $p = 0.004$) and canopy (LRT = 124.0, $p = 0.022$) order-level community composition differed significantly after replanting. On the ground, arthropod order-level community composition in all post-replanted cohorts differed significantly from Age *M* and from each other ($p < 0.05$ for all post-hoc comparisons; Figure 3b-Left). Univariate analyses indicated that reduced coleopteran abundances (LRT = 30.668, $p = 0.011$) in Ages 1 and 3 were the primary drivers of these differences (Figure S3). A similar effect was observed in the understorey ($p < 0.05$ for all post-hoc comparisons; Figure 3b-Centre), with increased abundances in Coleoptera (LRT = 21.435, $p = 0.029$), Hemiptera (LRT = 38.596, $p = 0.001$) and Psocoptera (LRT = 20.331, $p = 0.029$) in Age 1 driving these differences (Figure S4). Although

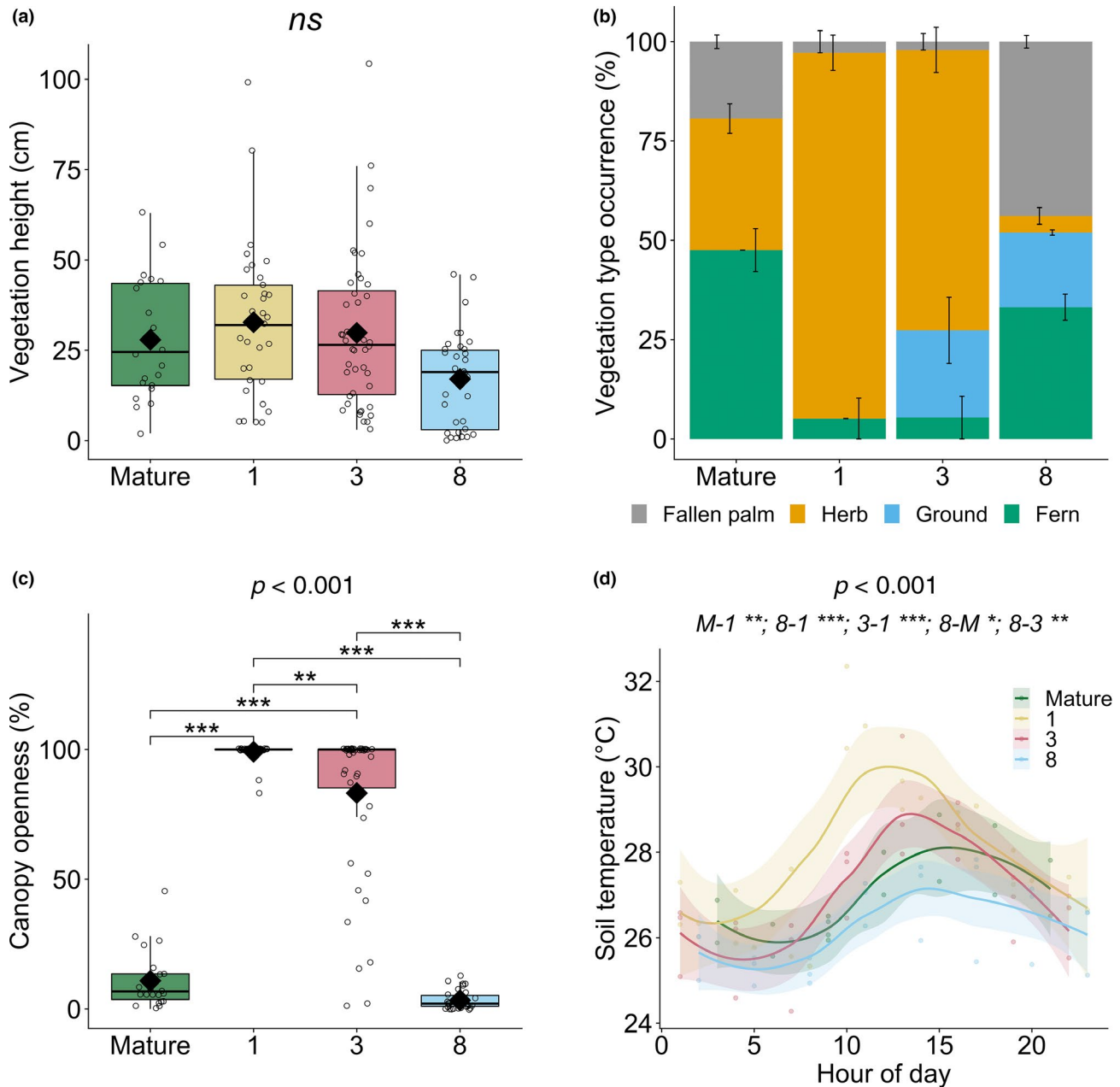


FIGURE 2 Differences in understory vegetation height (a), understory vegetation composition (b), canopy openness (c) and soil temperature (d) across studied oil palm age cohorts (*Mature*, *Age 1*, *Age 3*, *Age 8*). For (a) and (c), boxplots display median and interquartile ranges, raw data are shown in grey circles, and black diamonds indicate observed means. For (b), error bars represent the standard errors of means. For (d), lines represent outputs from the generalized additive model (with 95% confidence intervals), and raw data are shown as circles with colours indicating the associated cohort. The significance of cohort in each model (a, c, d) is indicated above the plots in text and, when cohort was significant, we indicate cohorts between which significant differences occurred: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = cohort not significant in the model. For (c), we present significance as per our initial model (i.e. we do not present significance as indicated by our sensitivity analysis, in which we tested the influence of nine extreme canopy openness data points in *Age 3* on our initial model findings)

our analyses indicated that cohort significantly influenced canopy order-level community composition, post-hoc comparisons did not indicate significant pairwise differences between cohorts ($p > 0.05$ for all; Figure 3b-Right). Univariate analyses indicated that lowered abundances in *Dermaptera* (LRT = 17.331, $p = 0.050$) and *Lepidoptera* (LRT = 25.449, $p = 0.008$) in *Ages 1* and *3* were the primary drivers of the overall significant difference (Figure S5).

3.3 | Impacts of replanting on spiders

We collected 338 spiders from the ground ($n_{\text{adults}} = 178$; $n_{\text{species}} = 38$; Appendix 1), 848 spiders from the understory ($n_{\text{adults}} = 300$; $n_{\text{species}} = 52$; Appendix 1) and 450 spiders from the canopy ($n_{\text{adults}} = 98$; $n_{\text{species}} = 52$; Appendix 1). Species accumulation curves in all microhabitats were starting to asymptote, indicating that our

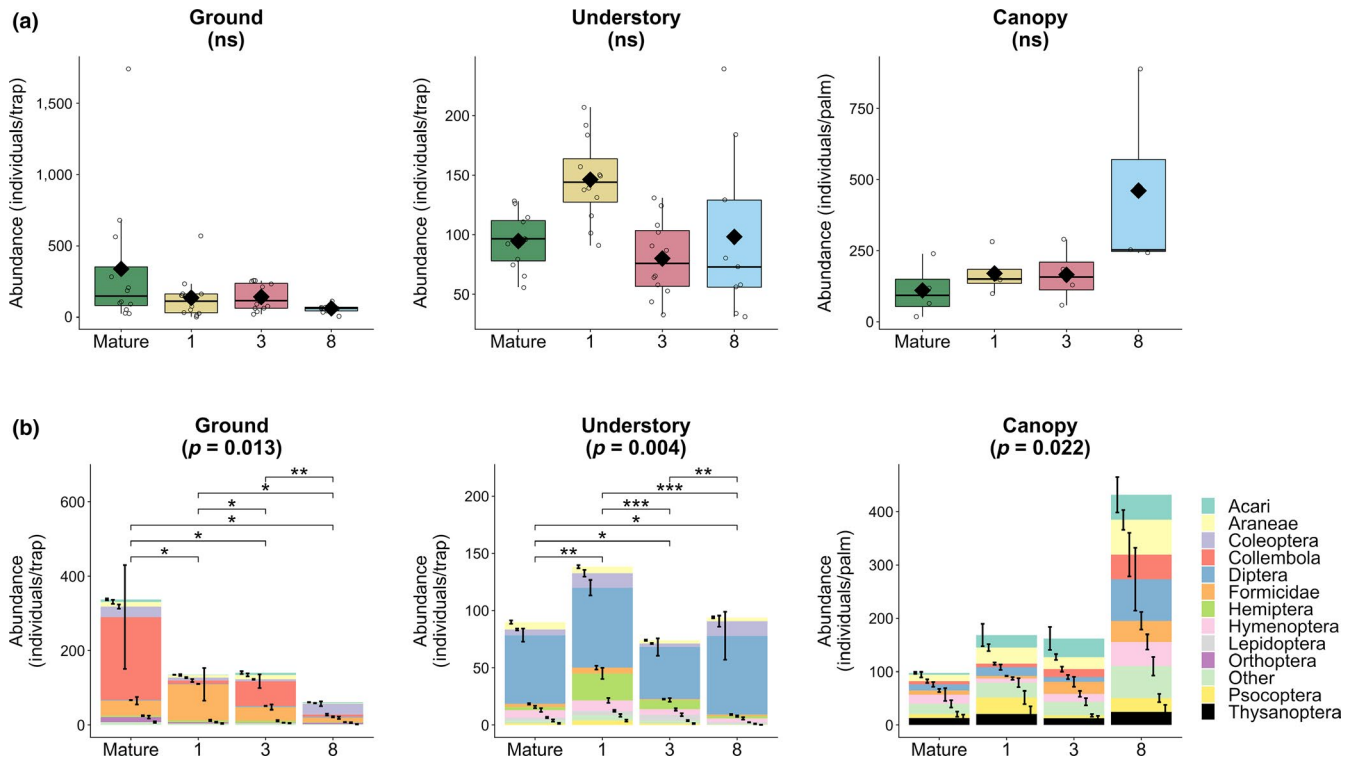


FIGURE 3 Differences in total abundance (a) and order-level community composition (b) for ground (Left), understory (Centre) and canopy (Right) arthropods across studied age cohorts (*Mature*, *Age 1*, *Age 3*, *Age 8*). The significance of cohort in each model is indicated above the plots in text and, when cohort was significant, we indicate cohorts between which significant differences occurred: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = cohort not significant in the model. In (a), boxplots display medians and interquartile ranges, raw data are shown in grey circles, and black diamonds indicate observed means. In (b), orders are plotted as they are sequenced in the legend, and error bars indicate one standard error from the mean

sampling of species was nearing completion within each microhabitat (Figure S6).

Replanting did not affect ground spider abundance (Ground spider abundance: $LRT = 4.473$, $p = 0.215$; Figure 4a-Left; Tables S10 and S11) or species richness (Ground spider species richness: $LRT = 6.880$, $p = 0.076$; Figure 4b-Left; Tables S10 and S11). Replanting affected both understory spider abundance ($\chi^2 = 9.675$; $p = 0.020$; Figure 4a-Centre; Tables S10 and S11) and species richness ($\chi^2 = 8.507$; $p = 0.040$; Figure 4b-Centre; Tables S10 and S11). Per transect, *Age 1* had ~50 fewer understory spider individuals ($p = 0.006$; Table S12) and ~7 fewer understory spider species ($p = 0.023$; Table S13) than *Age M*. Replanting also impacted canopy spider abundance ($\chi^2 = 7.787$; $p = 0.050$; Figure 4a-Right; Tables S10 and S11) and species richness ($\chi^2 = 7.870$; $p = 0.050$; Figure 4b-Right; Tables S10 and S11). Per palm, *Age 8* had ~50 more canopy spider individuals ($p = 0.019$; Table S14) and ~8 more canopy spider species ($p = 0.017$; Table S15) than *Age M*.

Ground ($LRT = 163.5$, $p = 0.014$), understory ($LRT = 275.8$, $p < 0.001$) and canopy ($LRT = 195.3$, $p = 0.004$) species-level community composition changed significantly after replanting (Table S16). On the ground, community composition in all post-replanted cohorts differed significantly from *Age M*, and the community composition in *Age 1* differed from that in *Age 3* (Figure 4c-Left). Univariate analyses indicated that four spider species (two species each of Oonopidae

and Lycosidae) were the primary drivers of these differences ($p < 0.05$ for univariate analyses; Appendix 1). In the understory, species-level community composition in *Ages 1* and *3* differed significantly from *Age M*, although *Age M* did not differ significantly from *Age 8*. Species-level community composition in all post-replanted cohorts differed significantly from each other (Figure 4c-Centre). Univariate analyses indicated that nine spider species (five species of Araneidae, three species of Tetragnathidae and one species of Theridiidae) were the primary drivers of these differences ($p < 0.05$ for univariate analyses; Appendix 1). In the canopy, community composition in *Age 1* differed significantly from *Age 8*, but there were no other significant differences between cohorts (Figure 4c-Right). Univariate analyses indicated that 11 spider species (three species of Araneidae, one species of Linyphiidae, three species of Oonopidae, one species of Tetragnathidae, two species of Theridiidae and one species of Thomisidae) were the primary drivers of these differences ($p < 0.05$ for univariate analyses; Appendix 1).

4 | DISCUSSION

In this study, we investigated changes in environmental conditions and arthropod communities across an oil palm chronosequence, to determine the impacts of replanting on oil palm landscapes over an 8-year

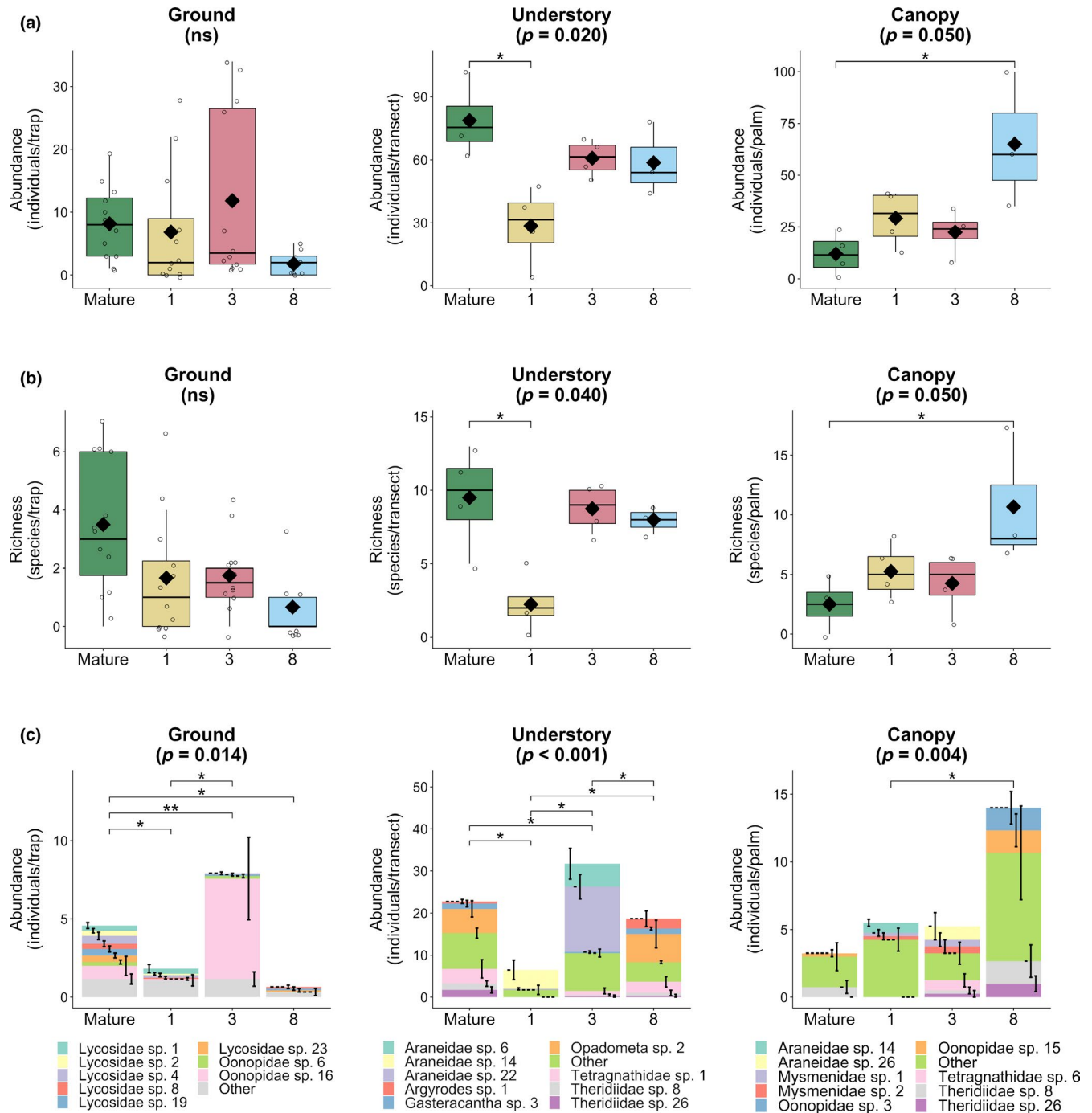


FIGURE 4 Differences in abundance (a), species richness (b) and species-level community composition (c) for ground (Left), understorey (Centre) and canopy (Right) spiders across age cohorts (Mature, Age 1, Age 3, Age 8). The significance of cohort in each model is indicated above the plots in text and, when cohort was significant, we indicate cohorts between which significant differences occurred: ** $p < 0.01$, * $p < 0.05$, *ns* = cohort not significant in the model. In (a and b), boxplots display medians and interquartile ranges, raw data are shown in grey circles, and black diamonds indicate observed means. In (c), only the nine most abundant species in each microhabitat are plotted, for ease of interpretation. Only the eight most abundant species are plotted in (c)-Left, owing to several species having equal abundances after the 8th most abundant species. Species are plotted as they are sequenced in their respective legends. Error bars indicate one standard error from the mean

period following replanting. Replanting in our study area was carried out using recommended industry replanting strategies, and is therefore likely to be comparable to how replanting has happened, or will soon happen, in industrial oil palm estates across Southeast Asia. Across the chronosequence, we found substantial changes in understorey

vegetation composition, canopy openness and soil temperature, but we did not find changes in understorey vegetation height. We also found differences in arthropod order-level community composition, spider abundance and species richness in the understorey and canopy, and spider species-level community composition in all microhabitats.

We found no significant differences in total arthropod abundance, or ground spider abundance and species richness.

4.1 | Impacts of replanting on the environment

Replanting of oil palm changed microclimate and understorey vegetation, with some changes still present even 8 years after replanting. The largest environmental differences occurred in two phases: between *Ages M* and 1, and between *Ages 3* and 8. Between *Age M* and *Age 1* (i.e. the period when first-generation mature palms were replaced by young replanted palms), an understorey vegetation community dominated by ferns was replaced by cover crop, a closed canopy became almost fully open, and soil temperatures increased and became more variable across the day. It is likely that replanting also changed other aspects of the ecosystem that were beyond the scope of this study, such as soil humidity and compaction. Between *Age 3* and *Age 8* (i.e. the period when young replanted palms grew into maturity), environmental conditions shifted back towards pre-replanting conditions. In comparison to the other cohorts, the environmental conditions in *Age 8* resembled those in *Age M* and, even where differences occurred, *Age 8* was more similar to *Age M* than to *Ages 1* and 3. We note that, in comparison to our initial canopy openness model, our sensitivity analysis indicated that, away from palm trunks (i.e. the majority of the *Age 3* landscape), openness in *Ages 1* and 3 was similar. Additionally, our sensitivity analysis found that *Age 8* had a more closed canopy than *Age M* (our initial model found no differences in openness between these cohorts). This difference may be partially explained by variation in management between *Ages M* and 8. For example, canopy fronds in *Age M* are often cut so that palm fruits can be more easily harvested, creating small gaps in the canopy, but this is not done in *Age 8*. Additionally, as a result of being older, occasional palms in *Age M* are more likely to be dead or dying than in *Age 8*, leading to gaps in the canopy at larger scales. Replanting did not affect understorey vegetation height. We attribute this to changes in vegetation composition related to replanting, which enabled different types of plants to produce similar vegetation height across the chronosequence. It is also likely that replanting changed other aspects of vegetation. For example, a previous study found that plant species richness and percent vegetation coverage increased in the first year after replanting before returning to pre-replanting levels within 3 years (Ashton-Butt et al., 2019). Our findings reflect previous research that documented changes in environmental conditions and processes across the oil palm life cycle (Hamilton, Trimmer, Bradley, & Pinay, 2016; Luskin & Potts, 2011; Pauli et al., 2014; Röhl et al., 2015). This indicates that, as second-generation oil palms age, environmental conditions may follow similar patterns of development as has previously been documented in first-generation plantations.

4.2 | Impacts of replanting on arthropods

We recorded 24 arthropod orders or other groups, and 131 spider morphospecies from 20 families, across ground, understorey and

canopy microhabitats within oil palm. Our findings show that, although significantly less biodiverse than natural forests (Drescher et al., 2016; Foster et al., 2011; Potapov, Dupérré, et al., 2020), oil palm plantations can harbour a broad range of taxa. Encouragingly, we found that replanting had little short-term (i.e. 1–3 years) or long-term (i.e. 8 years) negative impacts on total arthropod abundance in any microhabitat, as we found no significant differences in total arthropod abundance across the studied chronosequence and found relatively high arthropod abundances in all cohorts. This is likely to be explained by oil palm being primarily populated by generalist arthropod taxa that adapt easily to changes in microclimate and vegetation complexity (Chey, 2006; Chung, Eggleton, Speight, Hammond, & Chey, 2000; Fayle, Edwards, Foster, Yusah, & Turner, 2015). However, we also found that replanting changed arthropod order-level composition, altered spider species-level composition, and decreased spider abundance and species richness in some microhabitats.

4.2.1 | Impacts of replanting on the ground

On the ground, we found that replanting did not affect total arthropod abundance but changed arthropod order-level composition, owing to significant decreases in Coleoptera abundance after replanting. Our spider-focussed analyses showed similar trends, as replanting did not affect ground spider abundance or species richness, but changed species-level composition. Our findings reflect those of another study that occurred over a similar replanting period and focussed on soil macrofauna (Ashton-Butt et al., 2019), a community that is likely to exhibit similar patterns to surface-dwelling ground arthropods. This study found that replanting caused short-term (i.e. 1 month) declines in soil macrofauna abundance, although abundance recovered to pre-replanting levels within 1 year after replanting. Similar to our study, Ashton-Butt et al. (2019) also found that replanting caused long-term (i.e. 7 years after replanting) changes in soil arthropod order-level composition.

Coleoptera was the only ground-dwelling taxon affected by replanting, with decreases in Coleoptera abundance in the first 3 years after replanting. This could be due to a lack of dead palm fronds on the ground during this time period. Dead palm fronds are abundant on the ground in mature plantations, but not in young plantations, and can be an important habitat for ground-dwelling invertebrates (Wong et al., 2016). We suggest that the otherwise limited impacts of replanting on other ground arthropods may be attributed to management decisions that are implemented immediately after replanting. For instance, a cover crop was planted within 2 months of replanting in the plantations in which we sampled. Cover crops are primarily planted to reduce soil erosion after replanting, but they may also benefit arthropod biodiversity within agricultural systems. For instance, a previous study occurring in maize found that planting a cover crop increased soil macrofauna diversity and biomass (Blanchart et al., 2006). It is also noteworthy that the established management practice in the plantations in which we worked was to chop mature palms after clearance and leave them as mulch in the

post-replanting landscape. This practise provides additional habitat for ground arthropods, may provide more suitable microclimatic conditions than surrounding replanted areas and may partially compensate for the loss of palm fronds.

4.2.2 | Impacts of replanting in the understory

We found that replanting did not affect total arthropod abundance in the understory but changed arthropod order-level composition (owing to significant increases in Coleoptera, Hemiptera and Psocoptera in the first year after replanting). We also found that replanting significantly decreased the abundance and species richness of understory spiders in the first year after replanting, and additionally changed spider species-level community composition.

The post-replanting changes in understory arthropods that we observed are likely to be related to differences in vegetation composition across the chronosequence. Replanting resulted in a fern-dominated understory being replaced by cover crop and other herbaceous plants, which may have benefited some arthropods. For instance, the post-replanting rise in Hemiptera and Coleoptera abundance could be related to the increased density of herbaceous plants in *Age 1*, which could provide additional food sources for plant and insect-feeding species within these groups. Understorey vegetation that was killed during replanting and is decomposing in *Age 1* could be an important food source for Psocoptera, possibly explaining their post-replanting rise in abundance. The majority of understory spiders that we collected were orb-weavers (Araneidae and Tetragnathidae), which depend on structurally complex and stable vegetation to build their webs (Greenstone, 1984; Rypstra, 1983). In comparison to cover crop, ferns have greater structural integrity and complexity, potentially affecting the ability or proclivity of orb-weavers to inhabit them. It is also noteworthy that fern fronds curl distally, and we observed during our fieldwork that orb-weavers often retreated to these distal spaces while not feeding or when threatened. By comparison, we did not observe spiders in retreats under cover crop leaves. Although we did not quantify the association between understory vegetation composition and orb-weavers, our hypothesis is supported by a previous study that found that areas of mature palm with standard or enhanced levels of understory vegetation supported more understory spiders, and a different assemblage of understory spiders, to areas with reduced levels of vegetation (Spear, 2016). We do not attribute the changes in understory spider abundance or species richness that we observed to altered prey availability, since we found that total arthropod abundance in the understory did not change significantly after replanting.

4.2.3 | Impacts of replanting in the canopy

As in the ground and understory, replanting did not affect total arthropod abundance in the canopy, but changed arthropod order-level composition, owing to reduced abundances of Dermaptera and

Lepidoptera in the first 3 years after replanting. We also found that replanting significantly changed canopy spider species-level composition, and that canopy spider abundance and species richness was significantly higher in *Age 8* than *Age M*. However, our canopy spider abundance and species richness findings were only weakly significant ($p = 0.050$). Therefore, we recommend caution in interpreting these results.

The significant declines in Dermaptera and Lepidoptera after replanting may be attributed to reduced trunk and canopy complexity in young palms. For example, previous studies have found that frond axils, which are only found on mature palm trunks, can host abundant arthropod communities (Ganser, Denmead, Clough, Buchori, & Tschartke, 2017; Potapov, Bonnier, et al., 2020). We found that the abundance of canopy arthropods was particularly high 8 years after replanting, although trends were not always significant. This could be attributed to epiphytes, which are only found on the trunks of mature oil palms (i.e. they are not present on the trunks of *Age 1* and *Age 3* palms), but gradually decline in abundance as oil palms pass peak yields and the bases of fallen fronds rot away on the trunk. Such epiphytes can support high densities of arthropods in oil palm (Ganser et al., 2017; Turner & Foster, 2009), potentially explaining the high numbers of arthropods found in *Age 8* palms in this study.

We found relatively few ants in our canopy samples compared to other studies, particularly prior to replanting (i.e. *Age M*, where we found ~7 ants per fogging sample, representing ~7% of all arthropods that were collected). For instance, Turner and Foster (2009) found ~200 ants per fogging sample (~41% of all arthropods that were collected) in mature oil palm in Malaysia, and Hood (2019) found ~120 ants per fogging sample (~40% of all arthropods that were collected) in mature palms in the same plantation in which we sampled. Had ants been similarly abundant in our sites as they were in these studies, we could have observed more substantial changes in arthropod order-level community composition in the canopy, and possibly observed decreases in total canopy arthropod abundance after replanting. It is possible that the fewer ants that we found were due to differences in climate between our study and others. For instance, a previous study found that prolonged rainfall could reduce the abundance of ants in tropical forest canopies (Adis, 1988), and our canopy sampling occurred towards the end of the regional rainy season.

4.3 | Overall impacts of replanting, and implications for ecosystem functioning

Our analyses show that some aspects of arthropod biodiversity, such as total arthropod abundance, showed consistent trends across microhabitats. However, other aspects of biodiversity showed microhabitat-specific trends, suggesting that replanting differently impacted arthropods within the ground, understory and canopy. For instance, immediately (i.e. 1 year) after replanting, the abundance of spiders in the understory declined, but spider abundance on the ground and in the canopy remained unchanged. These findings

demonstrate that some aspects of the ground, understorey and canopy are differently impacted by replanting and subsequent management decisions in second-generation plantations. This can partially be explained by some management decisions specifically targeting a single microhabitat, for instance, herbicides that are applied to understorey vegetation will have a greater impact on understorey arthropods than arthropods in the canopy. Collectively, our microhabitat-specific analyses demonstrate that a single-microhabitat approach could offer a limited, or possibly biased, understanding of oil palm ecosystems. Our findings therefore underscore the importance of taking a whole-ecosystem approach when assessing the impacts of management on biodiversity within oil palm plantations.

The changes in composition, and declines in abundance of ground-inhabiting coleopterans, canopy-inhabiting lepidopterans and dermapterans, and declines in abundance and species richness of understorey spiders that we observed in this study could result in changes in a range of ecosystem functions. These include functions that impact growth and production of oil palms such as pollination, predation, decomposition and nutrient recycling, for which arthropods play key roles. For instance, some ground-inhabiting beetles contribute to dung removal (Gray et al., 2014) in oil palm plantations, and web-building spiders are important predators of pests in various agricultural systems (Michalko et al., 2019). It is also noteworthy that some arthropods are pests, such as caterpillars that eat the fronds of oil palms (Corley & Tinker, 2016). However, the impacts of replanting on ecosystem functioning in oil palm plantations may be limited, as a previous study found no short-term (i.e. 1–4 years) impacts of replanting on dung removal, soil mesofauna feeding activity, herbivore predation, seed predation or average multifunctionality (Woodham et al., 2019). To date, herbivory is the only ecosystem function that is known to change after replanting, and has been found to increase in the first 4 years after replanting but to return to pre-replanting levels within 8 years (Waters, 2018; Woodham et al., 2019). It is possible that this lack of difference is related to the lack of overall change in arthropod number that we found in this study and that, despite individual differences within orders, the arthropod community is relatively robust and able to deliver associated ecosystem functions across replanting events.

4.4 | Relevance to oil palm management

The oil palm estates in which this study occurred were replanted using recommended strategies, which included staggering replanting events to promote landscape-level heterogeneity across the plantation, retaining mature oil palm riparian buffers, planting a cover crop <2 months after replanting, and using chopped mature palms as mulch for young second-generation palms. After replanting, the estates were managed in accordance with sustainable growth guidelines from three independent certification bodies: Roundtable on Sustainable Palm Oil (RSPO), Indonesian Sustainable Palm Oil (ISPO) and International Sustainability & Carbon Certification (ISCC). Compliance with these strategies and growth guidelines is likely to

be comparable to how replanting and regrowth will happen, or has already happened, in industrial oil palm estates across Southeast Asia. To these ends, the findings of this study give valuable information about the effects of current sustainable growth guidelines, such as those provided by the RSPO, ISPO and ISCC. Importantly, we did not test the impacts of any singular strategy, and we highlight that this research is urgently required. Examples of such research initiatives are the *Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project*, which is testing how riparian buffer quality affects biodiversity, ecosystem processes and yields across oil palm replanting events (Luke, Advento, Aryawan, et al. 2020) and the *Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems (EFForTS) Project*, which is testing the impacts of different fertilizer and herbicide regimes on oil palm ecosystems (Darras et al., 2019).

5 | CONCLUSIONS

Across our sampled chronosequence, we found no differences in total ground, understorey or canopy arthropod abundance or the abundance and species richness of ground spiders, which assuages previously raised concerns (e.g. Snaddon et al., 2013) that replanting could devastate arthropod communities in oil palm ecosystems. However, we also found changes in arthropod order-level community composition and spider species-level community composition in all microhabitats, and differences in spider abundance and species richness in the understorey and canopy. Owing to these latter findings, our results are only somewhat encouraging for the long-term persistence of arthropods in oil palm plantations, and of the functions they can support. To these ends, this study is a useful baseline in determining how replanting using recommended strategies impacts oil palm ecosystems. We highlight that future research is needed, such as assessing the impacts of replanting on other taxonomic groups and quantifying the effects of individual replanting strategies, before the full long-term impacts of replanting on existing oil palm plantations can be understood.

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CONFLICT OF INTEREST

Co-authors with a Sinar Mas Agro Resources and Technology Research Institute (SMARTRI) affiliation were employed by SMARTRI, the research division of Golden Agri Resources (GAR), while research was conducted. SMARTRI and the University of Cambridge share a Memorandum of Understanding that protects the intellectual property rights and data-use for all researchers involved in this study. This research is therefore a collaboration between the University of Cambridge and GAR.

AUTHORS' CONTRIBUTIONS

M.D.P. led data collection (with assistance from A.A.K.A. and H.S.W.), identification of arthropods and spiders, statistical analyses and writing of the manuscript; M.D.P., H.S.W., A.A.K.A., S.H.L. and E.C.T. designed the study; M.D.P., A.A.K.A., S.H.L., N.D., M.N., J.-P.C. and E.C.T. contributed to the design of terrestrial arthropod sampling and identification protocols. All authors approved the manuscript.

DATA AVAILABILITY STATEMENT

Data available via the University of Cambridge Online Digital Repository <https://doi.org/10.17863/CAM.56212> (Pashkevich et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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