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**Spiders in canopy and ground microhabitats are robust to changes in understory
vegetation management practices in mature oil palm plantations (Riau, Indonesia)**

Running Title: Spiders and understory complexity in oil palm

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Abstract

Conversion of natural habitats to oil palm agriculture has caused declines in biodiversity and changes in ecosystem functions. To preserve biodiversity we must protect natural habitats, but once oil palm plantations are established, developing more-environmentally friendly management strategies could support higher levels of within-plantation biodiversity and boost the delivery of ecosystem services, possibly increasing oil palm productivity. In this study, we use a before-after control-impact (BACI) experiment to test whether three understory vegetation management strategies affect spider abundance, species richness, and species-level community composition in the canopy and ground microhabitats in mature oil palm plantations. Our treatments encompassed the range of current management practices and included heavy applications of herbicides to eliminate all understory vegetation, maintaining some understory vegetation using business-as-usual herbicide applications, and enhancing understory vegetation by not applying any herbicides. We focussed on spiders, as they are both biologically and economically important in oil palm plantations, owing to their important pest control services. We identified more than 1000 spiders, representing 20 families and 83 morphospecies. The treatments did not affect any aspects of spider biodiversity, although the abundance and species richness of canopy-dwelling spiders changed between pre- and post-treatment sample periods, independent of treatment. Our findings indicate that differences in understory vegetation management practices do not affect spiders, or the pest management services that they provide, in mature oil palm plantations. As such, more extreme changes in management would probably be required to enhance spider biodiversity in oil palm plantations in the long-term. Further studies are needed to determine the practicalities of such approaches, to assess how changes in vegetation management practices affect spiders in additional microhabitats, and how the impacts of such approaches vary across the 20-30 year oil palm commercial life cycle.

Introduction

Habitat conversion is a primary cause of biodiversity loss worldwide (Newbold et al., 2015). Tropical ecosystems are among the most vulnerable, owing in part to high rates of agricultural expansion and the inherently high levels of biodiversity that are found in tropical systems (Bradshaw et al., 2009; Kehoe et al., 2017). Expansion of oil palm (*Elaeis guineensis*) agriculture is a leading cause of habitat conversion in Southeast Asia (Koh & Wilcove, 2008) that has resulted in widespread species losses (Foster et al., 2011), and associated impacts on ecosystem functions (Dislich et al., 2017). Over the past two decades, more than 10 million hectares of land have been converted to oil palm plantation (FAO, 2019), the majority of which was tropical rainforest (Gibbs et al., 2010). Globally, oil palm agriculture is continuing to expand (Davis et al., 2020), making protection of remaining forest ecosystems a conservation priority (Gibson et al., 2011).

Once oil palm plantations are established, efforts can and should be taken to manage plantations more sustainably (Luke, Advento, et al., 2020). Changes in oil palm management can increase habitat heterogeneity within oil palm plantations and, consequently, support higher levels of biodiversity (e.g. Ashton-Butt et al., 2018; Luke et al., 2019; Zemp, Gérard, et al., 2019) and boost the delivery of ecosystem services such as pollination and pest control (Li et al., 2019; Turner & Hinsch, 2018), possibly increasing oil palm productivity (Gérard et al., 2017). Management strategies that can help to support higher levels of biodiversity in oil palm include retaining fragments of rainforest within oil palm landscapes at the time of plantation establishment (Lucey et al., 2014; Lucey & Hill, 2012), intercropping oil palm with other cash crops (e.g. Ashraf et al., 2018; Ghazali et al., 2016; Yahya et al., 2017), retaining riparian buffers made of rainforest at the time of plantation establishment (Gray et al., 2014; Williamson et al., 2021) or maintaining riparian buffers made of mature oil palms at the time of replanting

(Pashkevich et al., 2022; Woodham et al., 2019), enhancing the structural complexity and diversity of understory vegetation (e.g. Ashton-Butt et al., 2018; Darras et al., 2019; Luke, Advento, Aryawan, et al., 2020), and planting trees within the crop matrix (Teuscher et al., 2016; Zemp, Ehbrecht, et al., 2019; Zemp, Gérard, et al., 2019). Owing to their potential socioecological benefits, several of these management strategies are required for, or recommended by, leading sustainability certification organisation bodies such as the Roundtable on Sustainable Palm Oil ('RSPO'; RSPO, 2018).

Enhancing the structural complexity and diversity of understory vegetation in oil palm is a particularly promising and tractable strategy (Luke, Advento, et al., 2020). Depending on management, oil palm plantations can support a diverse assemblage of plants in the understory. For instance, 120 different species (representing 41 families) of flowering plants and ferns were found in mature oil palm plantations in Sumatra, Indonesia (Luke et al., 2019). At least 17 of these species were classed as beneficial for palm oil production (Luke et al., 2019). There are a wide range of understory vegetation management practices across oil palm growers, with some farmers eliminating understory vegetation using herbicides (owing to concerns that understory vegetation will compete with oil palms or make harvesting and access more difficult), others clearing only around palms and access paths, and others allowing understory vegetation to regrow. This is the case for both large-scale industrial plantations, and small-scale plantations that are owned by individual farmers ('smallholders'). Variation in understory management practices is likely to be higher in mature plantations, after standard plantings of cover crops in young plantations are cleared and non-cover crop plant communities self-establish (Corley & Tinker, 2016; Pashkevich et al., 2021). It is possible that maintaining structurally complex and diverse understory vegetation could lead to benefits for palm oil production, as understory vegetation can provide habitat for a range of functionally important

species that provide valuable ecosystem services (Turner & Hinsch, 2017). For instance, previous studies have found that maintaining understory vegetation can support higher abundances of leopard cats (*Prionailurus bengalensis* (Mammalia, Felidae)) that predate on rat pests (*Rattus rattus* (Mammalia, Muridae)) in oil palm (Hood et al., 2019), and ants (Insecta: Formicidae) that facilitate resource removal and could support pest control (Hood, Advento, et al., 2020).

Arthropods are abundant in most microhabitats in oil palm systems (e.g. Ashton-Butt et al., 2018; Pashkevich et al., 2021; Potapov, Dupérré, et al., 2020), and can affect palm oil production in a variety of ways. Whilst some arthropods, such as rhinoceros beetles (*Oryctes rhinoceros* (Coleoptera, Scarabaeidae)) and the larvae of bagworm moths (Lepidoptera, Psychidae), are pests and reduce palm oil production (Corley & Tinker, 2016), many others can benefit production by facilitating ecosystem services such as decomposition, pollination, nutrient cycling, and pest control (Dislich et al., 2017; Nurdiansyah et al., 2016). Spiders (Arachnida, Araneae) are one such important group of meso-predators that are abundant in oil palm (Pashkevich et al., 2021; Potapov, Dupérré, et al., 2020) and can contribute substantially to integrated pest management (IPM) in agricultural landscapes (Michalko et al., 2019). They sit near the top of invertebrate food chains and influence multitrophic interactions as both prey and predators (Nyffeler & Birkhofer, 2017). Previous studies have shown that spiders are responsive to changes in understory vegetation management. For instance, Neilly et al. (2020) found that increased cover of the understory shrub *Carissa ovata* (Gentianales, Apocynaceae) was associated with declines in spider abundance in Australian cattle pastures. Spear et al. (2018) found that removing understory vegetation in oil palm plantations caused declines in the abundance of kleptoparasitic spiders that inhabit the webs of *Nephila sp.* (Araneae, Araneidae). These results are likely to be influenced by both direct effects of habitat structure

(such as altering the amount of substrate available for web-building and nest-building; Halaj, Cady, & Uetz, 2000; Hood, Pashkevich, et al., 2020), and indirect effects via impacts on microclimate (Halaj et al., 2008), prey abundance (Pashkevich et al., 2021), and competition with other arachnid groups (Neilly et al., 2020). However, studies have not yet assessed the influence of varying understory vegetation management on spider communities across the range of microhabitats found in oil palm systems.

In this study, we used a replicated before-after control-impact (BACI) experiment (the Biodiversity and Ecosystem Function in Tropical Agriculture Understory Vegetation Project, or BEFTA-UVP) to test the effects of understory vegetation management on spiders in mature oil palm plantations. Specifically, we tested whether reducing, enhancing, or maintaining intermediate levels of understory vegetation through varying herbicide applications affected the abundance of all spiders, adults only, juveniles only; spider species richness; or spider species-level composition in the canopy and ground microhabitats of mature oil palm plantations.

Materials and methods

Study site

This study was conducted in Riau Province, Sumatra, Indonesia, as part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme. The BEFTA Programme is based in oil palm estates owned and managed by PT Ivo Mas Tunggal, a subsidiary company of Golden Agri Resources (GAR). The estates are managed semi-independently (Pashkevich et al., 2021), but with technical advice from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI), which is the research and development branch of GAR. See Luke, Advento, et al. (2020) for additional details on the BEFTA landscape and wider experimental framework.

Experimental design

Within the BEFTA Programme, this study occurred in the Understory Vegetation Project (BEFTA-UVP). The BEFTA-UVP is a large-scale, long-term understory vegetation manipulation experiment, which includes eighteen 150 x 150 m study plots, arranged in six triplets across two estates (“Kandista” and “Ujung Tanjung”) in the wider BEFTA landscape (Fig. 1). Plots were arranged such that the middle of each plot was 155 m from the outer edge of other plots in the triplet. Oil palms in all plots were planted between 1987 and 1993 and were therefore mature (20 – 26 years old), with an established canopy, at the time of this study. Experimental plots were established in October 2012, and experimental treatments were implemented in February 2014. The three experimental treatments were (from most intensive to least intensive management): high-input management, with intensive herbicide spraying and nearly complete loss of understory vegetation (“Reduced”); standard company practice, with intermediate herbicide spraying along harvesting paths and within 1.5 m radius circles around palms that kills off some, but not all, understory vegetation (“Normal”); and low-input

management, with no herbicide spraying but some manual cutting of woody vegetation along harvesting paths and within 1.5 m radius circles around palms, ultimately resulting in higher levels of understory vegetation (“Enhanced”) (see Appendix A: Fig. 1). Pre-treatment, all plots were managed following normal management practices. Treatments were assigned at random to plots within each triplet, so that each triplet had one plot of each treatment, and were maintained by re-applying herbicide regimes 3-5 times per year, or as necessary, throughout the study (Luke, Advento, et al., 2020). Treatments were effective in changing understory vegetation cover, biomass, and species richness, with per-plot plant species richness, biomass, and vegetation cover in ‘Reduced’ being significantly lower than in ‘Normal’ and ‘Enhanced’ after treatments were implemented (Table 1; Luke et al., 2019). For full details of the effects of the BEFTA-UVP treatments on understory vegetation, see Luke et al. (2019) and Luke, Advento, et al. (2020).

Sampling protocol

We sampled spiders living in the oil palm canopy and on the ground in a central 50 x 50 m area within each plot (Luke, Advento, et al., 2020). We sampled spiders from both canopy and ground microhabitats prior to treatment implementation (pre-treatment canopy: September 2013; pre-treatment ground: March 2013) and after treatment implementation (post-treatment canopy: September 2014; post-treatment ground: September 2014), allowing for a before-after control-impact (BACI) experimental design. Rainfall varied across the estates and sample periods (see Appendix A: Fig. 2).

We sampled spiders from the oil palm canopy using established insecticide fogging methods (see Appendix A: Fig. 3) (Pashkevich et al., 2021). Our fogging consisted of targeting one randomly-selected oil palm in each plot, and hanging six circular fogging trays (each consisting

of a loose cloth set across a 110 cm diameter frame) at breast height under the focal tree. Trays were hung either one or three metres away from the trunk of the focal palm in an alternating pattern, allowing capture of spiders from both the trunk and palm fronds. We used a densiometer (Lemmon, 1956) to measure canopy openness under each palm before fogging. We measured canopy openness in each of the cardinal directions, and converted these into a per-palm average. Fogging was conducted using a “Pulsefog Rolidor 25 EC” fogging machine filled with 7:1 diesel:insecticide (25 g L⁻¹ of synthetic pyrethroid insecticide with active ingredient “lambda cyhalothrin”), which was directed at the canopy for approximately 1.5 minutes. The operator moved around to compensate for wind and to ensure full coverage of the focal palm. Spiders were collected into bottles that hung from the centre of each tray and contained 75% ethanol. Bottles were collected about 2 hours after fogging, allowing sufficient time for spiders to fall from the canopy. Fogging was carried out between 06:45 and 10:00 to ensure minimal wind disturbance. Plots in two triplets were fogged each day and, therefore, it took three days to fog all BEFTA-UVP plots during a sampling period. The same palm was fogged before and after treatment implementation to enable direct comparison and to control for any impacts of variation between palms. While we are unaware of any studies in oil palm that have examined post-fogging recolonization of insects, studies in rainforest (Adis et al., 1998; Floren & Linsenmair, 1997) and eucalyptus plantations (Loch, 2005). indicate that one year between fogging is sufficient to allow most arthropods to recolonize the canopy.

We sampled ground-dwelling spiders using pitfall traps. Our traps were part of larger combination traps (also including an intercept trap and small Malaise trap at the top – not included in this study; see Appendix A: Fig. 3), which have previously been used successfully to sample a variety of arthropod fauna in human-modified landscapes in Southeast Asia (Ewers et al., 2015). The pitfall traps were made of a plastic funnel (23 cm in diameter), set flush to

the ground, with a small bottle of 75% ethanol at the bottom to catch and preserve spiders. We placed one pitfall trap at three points in each plot. Points were 31 m from the plot centre at 45°, 165°, and 285° bearings, and were therefore approximately 50 m apart and spaced at regular intervals around the plot centre. Traps were collected after three days, and spiders were stored in 75% ethanol. It took three weeks to set and collect pitfall traps across all BEFTA-UVP plots within a sampling period. Traps were placed in the same location before and after treatment implementation to enable direct comparison and to control for any impacts of variation within a plot.

After sampling, canopy- and ground-dwelling spiders were sorted from fogging and pitfall traps, and adult spiders were identified to family and sorted into morphospecies (identifying adults to genus or species when possible, using the relevant keys; Deeleman-Reinhold, 2001; Jocqué & Dippenaar-Schoeman, 2006; World Spider Catalog, 2021), with males and females included in each morphospecies (hereafter, 'species'). We could not reliably identify juveniles into species, so we only used juveniles for analyses of spider abundance. Spider samples are stored at SMARTRI and Pusat Penelitian Biologi, Lembaga Ilmu Pengetahuan Indonesia (LIPI; Bogor, Indonesia). We combined all fogging trays and pitfall traps in each plot to obtain per-plot measurements of canopy- and ground-dwelling spider biodiversity.

Statistical analyses

Characterising the BEFTA-UVP spider community

All analyses were conducted in R version 4.0.5 (R Core Team, 2021) using RStudio version 1.4.1106 (RStudio Team, 2021). Visualising our findings required *tidyverse* (Wickham, 2019). To characterise the studied spider community, we calculated interpolated and extrapolated species accumulation curves within each microhabitat (package *iNEXT*; Hsieh et al., 2016)

using the richness estimators derived by Chao et al. (2014). We extrapolated to double the number of collected individuals (Chao et al., 2014; Gotelli & Colwell, 2001). We also plotted rank abundance curves to assess species evenness within each microhabitat.

Effects of BEFTA-UVP treatments on spider abundance and species richness

We assessed effects of the BEFTA-UVP treatments on the abundance and species richness of adult canopy- and ground-dwelling spiders using generalised linear mixed effects models (GLMMs) (package *brms*; Bürkner, 2017), with the No-U-Turn sampler (NUTS) algorithm in Stan (Carpenter et al., 2017). For abundance analyses, we conducted separate tests on all spiders, adult spiders only, and juvenile spiders only.

We took an information theoretic approach to our modelling that involved fitting a series of five models for each response. This included a parent model ($Time * Treatment$, with ‘Time’ having levels ‘Pre’ and ‘Post’, and ‘Treatment’ having levels ‘Reduced’, ‘Normal’, and ‘Enhanced’), and four derivative models ($Time + Treatment$, $Time$ -only, $Treatment$ -only, and a null model). We included *Triplet* as a random effect in all models, to account for repeated samples within a triplet across time periods, and potential spatial autocorrelation. We initially fitted our GLMMs to poisson distributions (log links) and, if models were overdispersed, we re-fitted them to negative binomial distributions (log links). After generating and validating each series of models (see Appendix A: Text 1 for additional details), we calculated and compared each model’s exact leave-one-out cross-validation information criterion (LOOIC) (Gabry et al., 2019). We identified the model with the lowest LOOIC as the optimal model, except when the standard errors of the expected log pointwise predictive density (ELPD) of multiple models overlapped, in which case we chose the simplest model. When optimal models included *Time*, *Treatment*, or the interaction of these effects, we conducted post-hoc analyses

(package *emmeans*; Lenth et al., 2021) to determine factor levels that were meaningfully different (here understood to mean that the 95% highest posterior density (HPD) interval of the median point estimate calculated from our comparisons did not overlap with zero). We determined that *Treatment* affected the response if the optimal model included *Treatment*Time*, and posthoc analyses indicated meaningful differences between *Pre* and *Post* within a *Treatment*. We ran sensitivity analyses on our pre-treatment data to ensure that per-palm canopy openness did not affect the abundance and species richness of canopy-dwelling spiders (see Appendix A: Text 2), and therefore need to be included in our modelling. We did not run similar sensitivity analyses on ground spider data, as all local environmental variables (e.g. understory vegetation complexity) were collinear with *Treatment*.

Effects of BEFTA-UVP treatments on spider species-level composition

We assessed effects of the BEFTA-UVP treatments on the species-level composition of canopy- and ground-dwelling spiders using multivariate generalised linear models (mGLMs) (package *mvabund*; Wang et al., 2021). We fitted mGLMs to poisson distributions (log links) with the interaction of *Time*Treatment* as a fixed effect. We assessed the significance of *Time*Treatment* using likelihood ratio tests (LRTs) and by bootstrapping probability integral transform (PIT) residuals ($n_{\text{iterations}} = 10,000$), including *Triplet* as a blocking variable in these analyses, to account for repeated samples within a triplet across time periods, and potential spatial autocorrelation. If *Time*Treatment* was not significant ($P \geq 0.05$), we simplified our models using backwards stepwise model selection until only significant fixed effects, or an intercept-only model, remained. If the final model included fixed effects, we calculated pairwise differences between fixed effect levels, and ran univariate analyses to identify spider species that significantly differed in abundance. We visualised the findings of our mGLMs using stacked bar charts, and by plotting the posterior medians of Bayesian generalised linear

latent variable models (GLLVMs) as ordinations (package *boral*; Hui, 2021). GLLVMs and associated ordinations are model-based equivalents to distance-based multivariate visualisation tools, such as non-metric multidimensional scaling (NMDS). We fitted our GLLVMs to poisson distributions, included *Triplet* as a random effect (to account for repeated samples within a triplet across time periods, and potential spatial autocorrelation), and fitted two latent variables (allowing for two-dimension ordinations). See Appendix A: Text 1 for additional details on how we fitted and validated our mGLMs and GLLVMs. We ran a sensitivity analysis on our pre-treatment data to ensure that per-palm canopy openness did not affect the species-level composition of canopy-dwelling spiders (see Appendix A: Text 2), and therefore need to be included in our modelling. We did not run similar sensitivity analyses on ground spider data, as all local environmental variables (e.g. understory vegetation complexity) were collinear with *Treatment*.

Results

Characterising the BEFTA-UVP spider community

We collected 1128 spiders in total, including 615 spiders (177 adults across 54 species and 15 families; 438 juveniles) from the canopy, and 513 spiders (247 adults across 35 species and 10 families, and 266 juveniles) on the ground. The species accumulation curve for ground-dwelling spiders was starting to level-off, indicating that our sampling effort captured a large portion of species in this microhabitat (Fig. 2A). However, the species accumulation curve for canopy-dwelling spiders was still increasing, indicating that we captured a lower portion of canopy species relative to ground-dwelling spiders. Species accumulation curves for canopy and ground species increased at similar rates both pre- and post-treatment implementation, and across treatments, indicating that sampling completeness was consistent across all parts of the study (see Appendix A: Fig. 4). Three species from two families (*Araneidae sp. 1*, *Oonopidae*

sp. 1, and *Oonopidae sp. 2*) represented 52.5% of adult spiders found in the oil palm canopy, whilst four species from two families (*Lycosidae sp. 1*, *Lycosidae sp. 2*, *Lycosidae sp. 8*, and one species of an unknown family, *Unknown sp. 1*) represented 51.4% of adult spiders on the ground (Fig. 2B).

Effects of the BEFTA-UVP treatments on spiders in the canopy

In the canopy, the BEFTA-UVP treatments did not affect the abundance of either all spiders, adults only, or juveniles only. The optimal model for all three abundance analyses was the *Time*-only model, with abundance being lower post-treatment. Post-hoc analyses showed that, in comparison to post-treatment, the per-palm abundance of all spiders (Pre-treatment mean $(\bar{X}) \pm SE = 27.1 \pm 4.8$; Post-treatment $\bar{X} \pm SE = 7.1 \pm 1.3$), adults only (Pre-treatment $\bar{X} \pm SE = 7.8 \pm 1.3$; Post-treatment $\bar{X} \pm SE = 2.0 \pm 0.5$), and juveniles only (Pre-treatment $\bar{X} \pm SE = 19.2 \pm 3.6$; Post-treatment $\bar{X} \pm SE = 5.1 \pm 1.0$) was 3.8, 3.9, and 3.8 times higher pre-treatment, respectively (Fig. 3A-C). The BEFTA-UVP treatments also did not affect spider species richness in the canopy. The optimal model was the *Time*-only model, and richness was 2.8 times higher pre-treatment (Pre-treatment $\bar{X} \pm SE = 5.0 \pm 0.7$; Post-treatment $\bar{X} \pm SE = 1.8 \pm 0.4$; Fig. 3D). The BEFTA-UVP treatments did not affect spider species-level composition in the canopy, and the null model was the optimal model (Fig. 3E-F).

Effects of the BEFTA-UVP treatments on spiders on the ground

On the ground, the BEFTA-UVP treatments did not affect the abundance of either all spiders, adults only, or juveniles only (Fig. 4A-C); spider species richness (Fig. 4D); or spider species-level composition (Fig. 4E-F). Further, the optimal model for all analyses was the null model.

Discussion

In this study, we found 1128 spiders representing 82 species inhabiting the canopy and ground microhabitats in mature oil palm plantations. This indicates that, although likely less biodiverse than forest (e.g. working with ground-dwelling spiders, Potapov et al. (2020) found that oil palm plantations had up to 90% fewer spider individuals and 98% fewer species, in comparison to forest; comparing rainforest and oil palm canopies, Junggebauer et al. (2021) found no differences in the density or richness of Salticidae spiders), mature oil palm plantations can support relatively abundant and speciose spider assemblages. In both microhabitats, we found that changes in understory vegetation management practices did not significantly affect the abundance of either all spiders, adult spiders only, or juvenile spiders only; spider species richness; or spider species-level community composition. However, we found differences in the abundance and species richness of canopy-dwelling spiders, but not ground-dwelling spiders, between pre- and post-treatment sample periods.

The BEFTA-UVP spider community

We found a relatively abundant and diverse assemblage of spiders in the canopy and ground microhabitats in mature oil palm, in line with findings from other studies on spiders in Indonesian oil palm plantations. These studies have focussed on spiders in the canopy (Junggebauer et al., 2021; Pashkevich et al., 2021, 2022), understory (Pashkevich et al., 2021, 2022), leaf litter (Potapov, Dupérré, et al., 2020), ground (Pashkevich et al., 2021, 2022; Potapov, Dupérré, et al., 2020), and soil (Ashton-Butt et al., 2018; Potapov, Dupérré, et al., 2020) microhabitats, and also within termite mounds (Hood, Pashkevich, et al., 2020). The species accumulation curve for canopy-dwelling spiders was still increasing, indicating that we sampled only a portion of species within this microhabitat. The still-increasing curve may be attributed to our fogging of only one palm in each plot per sample period. In comparison, we placed three pitfall traps in each plot per sample period, and the species accumulation curve for

ground-dwelling spiders had flattened-out. That spiders are relatively abundant and species-rich in most microhabitats in oil palm plantations is unsurprising, as spiders are mostly generalist predators that are found in nearly all terrestrial habitats (Nyffeler & Birkhofer, 2017; Piel, 2018), and also because insect prey are common in oil palm systems (Pashkevich et al., 2021, 2022).

Spider communities in both the canopy and ground microhabitats were dominated by a few species. Dominant species in the canopy included orb-web builders (families Araneidae and Theridiosomatidae), cob-web builders (families Theridiidae and Dictynidae) and cursorial (i.e. running) hunters (family Oonopidae). All dominant species on the ground were cursorial hunters (families Lycosidae and Oonopidae). Overall, these findings indicate that oil palm plantations can harbour spiders with a relatively wide variety of life history strategies, suggesting that spiders occupy multiple niches within oil palm ecosystems. Web-building spiders in the canopy are likely benefitting from the structural complexity provided by oil palm fronds (Diehl et al., 2013). Oonopidae, a very understudied spider family (Jocqué & Dippenaar-Schoeman, 2006; <https://research.amnh.org/oonopidae/projectdescription/projectdetails.php>), has previously been found in high abundances in both canopy and ground microhabitats across the tropics (e.g. Chen & Tso, 2004; da Rocha Dias, Brescovit, & de Menezes, 2005; Pashkevich et al., 2021; Potapov, Dupérré, et al., 2020; Russel-Smith & Stork, 1994). Our results, alongside existing literature, suggest that Oonopidae may be an important group of spiders in disturbed habitats, meriting further research.

Effects of the BEFTA-UVP treatments

Spiders use understory vegetation for web-building (Diehl et al., 2013; Pashkevich et al., 2021), nesting sites (Lubin, 1978), protection from the sun (Balfour & Rypstra, 1998), hunting

(Pashkevich et al., 2021; Rinaldi & Forti, 1997) and, in some cases, for consumption as food (Nyffeler et al., 2016). The BEFTA-UVP treatments eliminated nearly all understory vegetation in 'Reduced' plots, and maintained or increased vegetation complexity and diversity in 'Normal' and 'Enhanced' plots (Luke et al., 2019; Luke, Advento, et al., 2020). Despite this, the BEFTA-UVP treatments did not affect the abundance of either all spiders, adult spiders only, or juvenile spiders only; spider species richness; or spider species-level community composition in the canopy or ground microhabitats.

It is perhaps not entirely unexpected that the BEFTA-UVP treatments did not have significant effects on the spiders in mature oil palm canopies. Oil palms in our study plots had canopies that were about 15 m above the understory vegetation layer. Therefore, changes in understory vegetation management may not have affected the canopy as a microhabitat for spiders. In addition, several microhabitats that support robust spider communities exist between the understory vegetation layer and the oil palm canopy, perhaps further suppressing effects of the BEFTA-UVP treatments on canopy-dwelling spiders. For instance, palms in our study plots had a relatively high density of epiphyte coverage (which was not targeted by the BEFTA-UVP treatments), and epiphytes are an important microhabitat in oil palm plantations that support arthropods including spiders (Turner & Foster, 2009). Similarly, the BEFTA-UVP treatments did not affect oil palm leaf axils and the space between and at the ends of oil palm leaflets (Potapov, Bonnier, et al., 2020), and spiders are known to inhabit these spaces (Ganser, Denmead, Clough, Buchori, & Tschardt, 2017; Potapov, Bonnier, et al., 2020; Personal Observation). The lack of an effect of treatment on canopy spiders could also be related to our incomplete sampling of the canopy community (with species accumulation curves for canopy-dwelling spiders still increasing), or the relatively low number of spider individuals that were collected in this microhabitat. However, it is noteworthy that the curves for canopy-dwelling

spiders were still increasing across all treatments, and rates of increase were similar both before and after treatments were implemented, making it less likely that we missed an effect of the BEFTA-UVP treatments on canopy-dwelling spiders.

In comparison to our canopy findings, it is more surprising that the BEFTA-UVP treatments did not affect spiders on the ground. Spiders in this microhabitat live directly amongst and below understory vegetation and, therefore, changes to understory vegetation management were expected to have impacts on ground-dwelling spider biodiversity. Our findings suggest that these spiders are utilising other aspects of vegetation complexity and diversity that were retained in study plots, regardless of BEFTA-UVP treatment. For instance, shade – which helps spiders to avoid desiccation by mitigating sun exposure (Balfour & Rypstra, 1998) – is provided partly by understory vegetation but also by the oil palm canopy in the BEFTA-UVP plots. Additionally, all plots retained complex habitats, such as cut frond piles, and termite mounds (Hood, Pashkevich, et al., 2020), which may provide habitat and shelter for ground-dwelling spiders. Cut palm fronds are present in all BEFTA-UVP treatment plots, and are stacked along harvesting paths in plantations and left to decompose (Luke, Advento, et al., 2020). They may therefore help to compensate for a lack of understory vegetation in ‘Reduced’ plots

Whilst we do not know whether the spiders we sampled were generalist or specialist species, owing partly to a general lack of knowledge about spider biology in Southeast Asia (Deeleman-Reinhold, 2001; Ramos-Gutierrez, 2020), it is likely that most spiders were generalist predators and tolerant to habitat disturbance, as specialist species were probably filtered out when forest was originally converted to oil palm plantation (Chung et al., 2000; Fayle et al., 2015). Such species are likely to be less affected by, and less responsive to, changes in management

practices, potentially further explaining why the overall spider community was relatively robust to changes in understory vegetation management practices. Additionally, many of the spiders that we found, including most spiders on the ground and Oonopidae in the oil palm canopy, were cursorial hunters and, therefore, were probably less affected by changes in understory vegetation than other spiders, such as web-builders, which rely more heavily on complex vegetation for habitat (Diehl et al., 2013). It is unlikely that the BEFTA-UVP treatments affected prey availability for spiders, as insect communities – which form the bulk of spider diet in oil palm – have been found to be remarkably robust to changes in management (Pashkevich et al., 2021). It is further possible that effects of the BEFTA-UVP treatments on ground-dwelling spiders were masked, owing to seasonal differences between pre- and post-treatment sampling. For pragmatic purposes related to our sampling schedule, our pre-treatment surveys of ground spiders occurred in March, but our post-treatment surveys occurred in September. Although regional air temperature is relatively consistent year-round (26 – 28 °C; Meijide et al., 2018), levels of rainfall did differ between pre- and post-treatment sample periods, possibly masking effects of the BEFTA-UVP treatments. However, given the BACI design of our experiment, we would have expected to have detected such a masking effect in our ‘Normal’ treatment plots, and we did not.

It is likely that the BEFTA-UVP treatments affected the biodiversity of spiders that live directly on, or build their webs between, understory vegetation, as previous studies in oil palm plantations have shown that spiders are abundant in this microhabitat, and affected by changes in management practices (Pashkevich et al., 2021, 2022; Spear et al., 2018). Sampling spiders in this microhabitat was not carried out in this study, and future research is therefore needed to determine whether changes in understory vegetation management practices in oil palm plantations affect these spiders.

Differences in spider communities across time

We found that the abundance of either all spiders, adults only, juveniles only, and spider species richness were lower in our second sampling period in the oil palm canopy. Species-level community composition in the canopy did not change, indicating that changes in relative within-species abundance over time were not substantial. We suggest that the drop in canopy-dwelling spider abundance and richness across all treatments may have been caused by climate effects that occurred between pre- and post-treatment sample periods. Rainfall differed between sample periods, and patterns of rainfall differed in the lead-up to sampling. Previous studies in oil palm plantations have shown that reduced rainfall reduces the biodiversity of arthropods, such as beetles (Insecta, Coleoptera) (Dhileepan, 1994) and dragonflies (Insecta, Odonata) (Luke, Advento, et al., 2020), making this a likely factor in the current study. However, we acknowledge that an influence of rainfall on spider communities is only speculative, and we did not directly test for this. Further research is needed to understand how variation in weather and climate affects spider communities in all microhabitats in oil palm plantations, and whether anthropogenic-associated climate change will affect oil palm spider communities over time. Although we are unaware of any such studies in oil palm, a study in the Caatinga biome in Brazil demonstrated that long-term patterns in rainfall were associated with spider abundance (Carvalho et al., 2015), and a study in tropical China found that drought reversed the effects of spiders on food webs in the leaf litter (Liu et al., 2015).

In comparison to spiders in the canopy, we did not find changes in the biodiversity of ground-dwelling spiders over time. This microhabitat-specific effect may be explained by spiders in the canopy being relatively more exposed to weather events and changes in climate. This is supported by a previous study in Jambi, Indonesia, which showed that a 2014-2015 drought

associated with the El Niño Southern Oscillation (ENSO) had fewer effects on microclimatic conditions below-canopy than outside the canopy (i.e. in open areas with no canopy; Meijide et al., 2018). However, as discussed previously, any effects of weather or climate on spiders in this study is speculative.

Management implications and directions for future research

The findings of this study have several management implications. We showed that, although less biodiverse than forest (Junggebauer et al., 2021; Potapov et al., 2020), mature oil palm plantations can support relatively abundant and speciose spider communities, which are robust to changes in oil palm management. On the one hand, this is encouraging from an ecological and oil palm productivity perspective, as spiders provide important pest control services within agricultural landscapes, and are therefore valuable to maintaining or increasing crop yields (Michalko et al., 2019). For instance, spiders in oil palm eat caterpillars of Psychidae moths (Lepidoptera), which are among the most economically harmful pests in oil palm plantations (Corley & Tinker, 2016). However, on the other hand, our findings indicate that maintaining high levels of understory vegetation (the “Enhanced” treatment in our study) does not give any additional increase in canopy- or ground-dwelling spider biodiversity (and likely the pest control services that spiders provide) in mature oil palm plantations. Additional efforts are, therefore, needed to identify management strategies that can be tractably implemented in oil palm to boost levels of spider biodiversity and their pest control services, without causing significant impacts on palm oil yields. Such strategies may include enrichment planting in the understory, altering the planting density of oil palm, intercropping oil palms with other cash crops, and leaving or restoring areas of native vegetation within the crop matrix. Effects of oil palm management practices such as these on spider biodiversity are being studied in the EFForTS Biodiversity Enrichment Experiment (EFForTS-BEE) Project in Jambi, Indonesia,

and the Riparian Ecosystem Restoration in Tropical Agriculture (RERTA) Project in Riau, Indonesia, which are assessing how planting of native forest trees in oil palm plantations affects biodiversity, ecosystem processes, and crop yields (Luke, Advento, et al., 2020; Teuscher et al., 2016).

It is noteworthy that this study occurred in mature oil palm plantations, as plantations of this age dominated our study area, are widespread across Southeast Asia owing to rapid regional expansion of oil palm plantations in the 1990s (Koh & Wilcove, 2008), and show particularly variable understory management. However, oil palm is a long-lived crop with a 20 - 30 year commercial life cycle (Corley & Tinker, 2016), and it is possible that the BEFTA-UVP treatments would affect canopy- and ground-dwelling spiders differently in different ages of oil palm with varying environmental conditions. For example, young oil palm plantations have a more open canopy and higher temperatures that are more variable across the day than older plantations (Pashkevich et al., 2021). Also, young oil palm plantations house different communities of spiders (Pashkevich et al., 2021), which may respond variably to changes in management. However, assessing the effects of different understory vegetation management practices on young oil palm systems is likely to be less relevant from a management point of view. This is because, understory vegetation management practices are usually fixed in these plantations, with most farmers choosing to plant dense, nitrogen-fixing cover crops during oil palm planting that persist until canopy closure, to provide valuable soil erosion and nutrient benefits (Corley & Tinker, 2016; Pashkevich et al., 2021). Future studies are needed to determine whether the lack of effect of the BEFTA-UVP treatments is consistent across the oil palm commercial life cycle. Such research will improve understanding of how spiders, and their pest control services, are affected by changes in environmental conditions and oil palm

management, supporting the development of more biodiverse and potentially more productive oil palm systems.

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Author Contributions

MDP analysed the data and wrote the manuscript (supported by DMS). ADA led the fieldwork. DMS identified the spiders. DMS, ADA, WAF, MN, J-PC, SHL, JLS, SP, and ECT designed the study, and contributed to the design of spider sampling and identification protocols. All authors reviewed and approved the manuscript.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at
XXXXX."

Declaration of interests

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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.

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Table 1. Effects of BEFTA-UVP treatments (Enhanced, Normal, Reduced) on the species richness, biomass, and percent cover of understory vegetation in study plots. We present data from both pre- (May – July 2013) and post-implementation (August 2014) of the BEFTA-UVP treatments. Values represent means \pm standard errors from ten 1 m² quadrats that were placed randomly in a central 50 x 50 m area of each plot. Findings show that the BEFTA-UVP experiment successfully altered understory vegetation, with the species richness, biomass, and percent cover of understory vegetation being substantially lower in Reduced plots, post-treatment, in comparison to Normal and Enhanced plots. Additional details on the effects of the BEFTA-UVP treatments on vegetation communities within plots can be found in Luke et al. (2019) and Luke, Advento, et al. (2020).

	<i>Enhanced</i>		<i>Normal</i>		<i>Reduced</i>	
	<i>Pre</i>	<i>Post</i>	<i>Pre</i>	<i>Post</i>	<i>Pre</i>	<i>Post</i>
<i>Species richness</i>	4.28 \pm 0.37	3.77 \pm 0.33	4.40 \pm 0.31	3.95 \pm 0.29	3.68 \pm 0.25	1.67 \pm 0.25
<i>Biomass (g)</i>	87.47 \pm 8.00	85.87 \pm 8.00	115.20 \pm 12.27	68.27 \pm 6.93	105.60 \pm 12.80	7.47 \pm 2.67
<i>Percent cover</i>	64.75 \pm 3.69	68.85 \pm 2.87	67.62 \pm 3.28	59.02 \pm 3.69	63.52 \pm 2.87	14.75 \pm 2.87

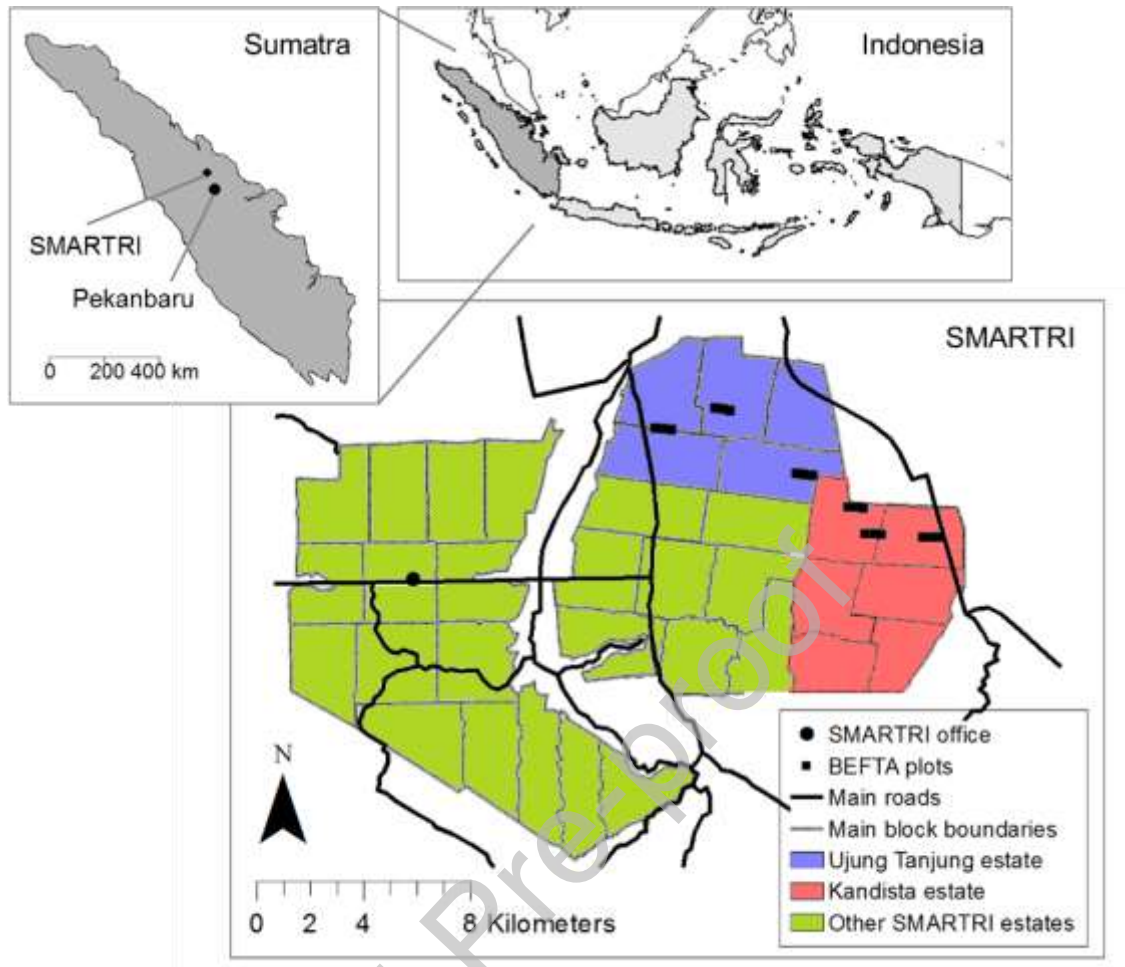


Fig. 1. Maps showing the location of the BEFTA-UVP in Sumatra, Indonesia. Experimental plots are arranged in triplets, and located across two oil palm estates (Ujung Tanjung, Kandista). Maps were reproduced from Luke et al. (2019), and were originally produced using the *maps* package (Brownrigg, 2021) in RStudio and ArcMap 10.5.1 GIS Software (ESRI, 2017).

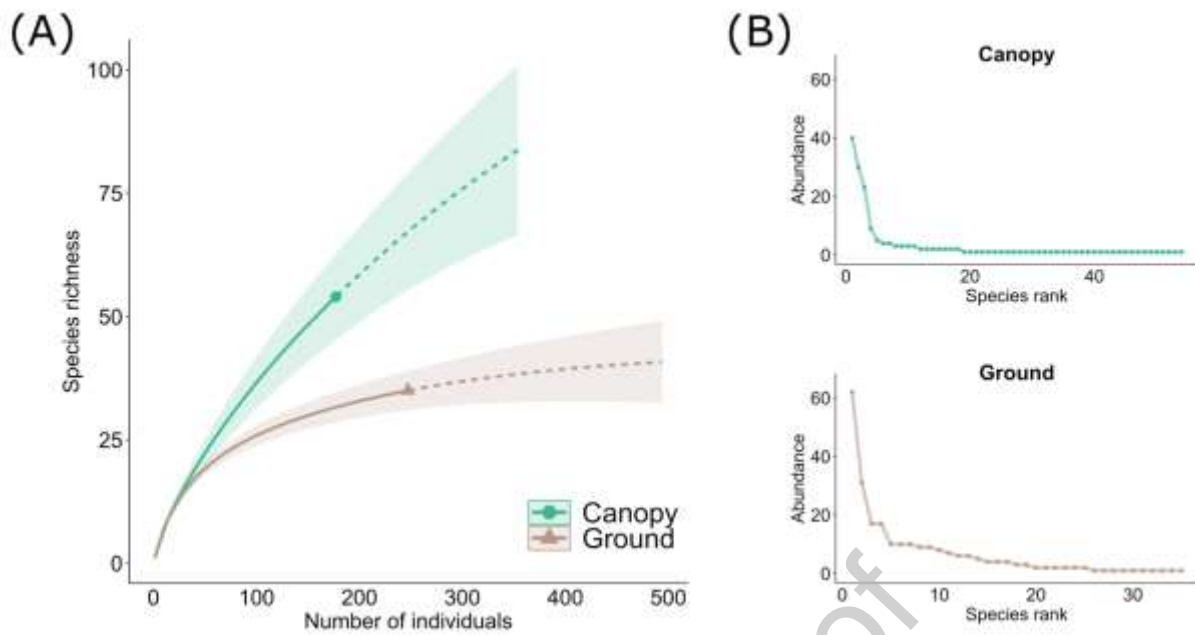


Fig. 2. Species accumulation (A) and rank abundance (B) curves for canopy- (green) and ground-dwelling (brown) spiders that were found across samples in the BEFTA-UVP landscape. For (A), we plotted both interpolated (solid line) and extrapolated (dotted line) curves. We extrapolated to double the number of collected individuals (Chao et al., 2014; Gotelli & Colwell, 2001).

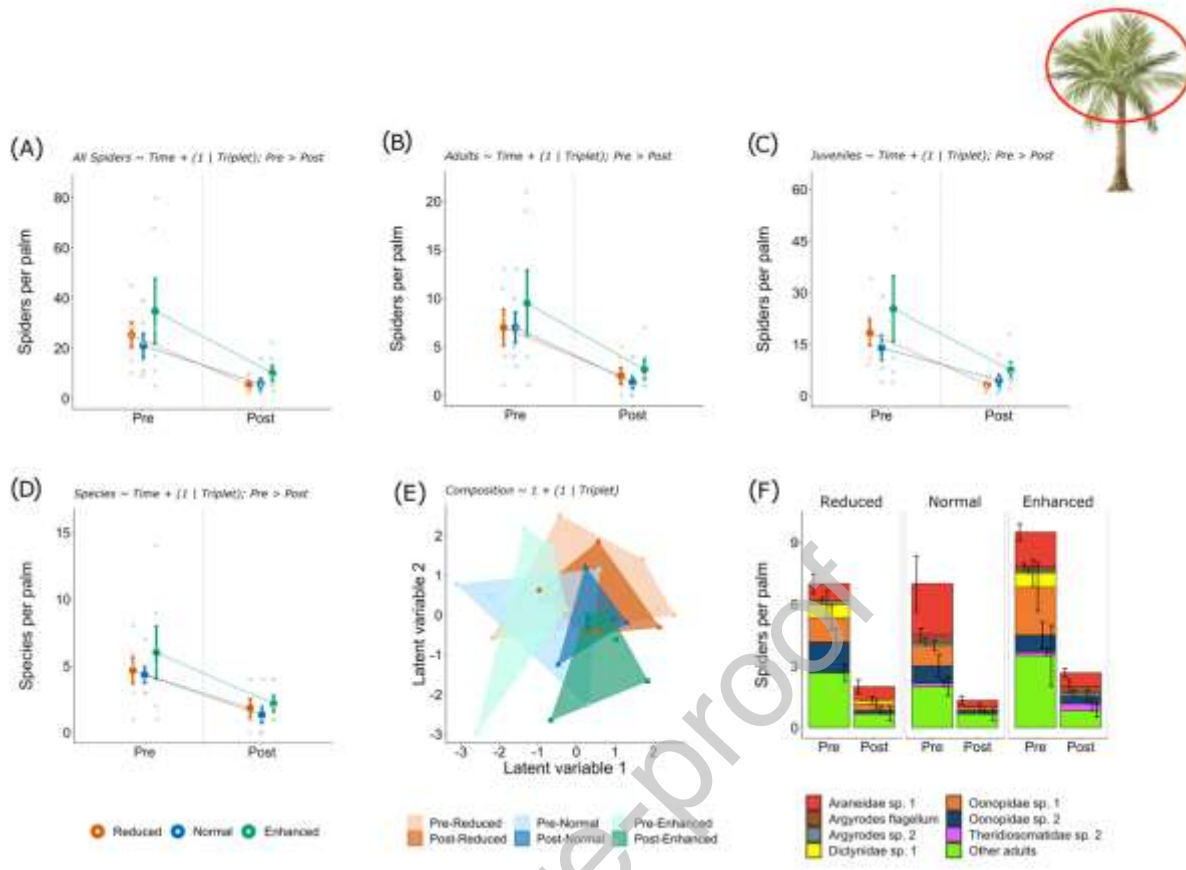


Fig. 3. Effects of the BEFTA-UVP treatments on the abundance of either all spiders (A), adults only (B), and juveniles only (C); spider species richness (D), and species-level composition (E & F) in the canopy. In (A)-(D), posterior distributions from GLMMs tracked to their underlying datasets; circles and error bars indicate pre- and post-treatment means and associated standard errors (1 standard error from the mean), respectively (Reduced = Orange; Normal = Blue; Enhanced = Green); and white circles indicate raw per-palm data. In (E), points represent the posterior medians of the GLLVM that we used to visualise the findings of our species-level composition analyses. Polygons were drawn around medians representing samples from the same *Time* and *Treatment* groups. In (F), error bars indicate one standard error from the mean, and spider species are plotted as they are sequenced in the legend. The 7 most abundant species across samples are plotted separately from other adults. In (A)-(E), we indicate the optimal model for each analysis, as determined by LOO-IC (A-D) or backwards stepwise model

selection (E). There is no optimal model listed for (F), as this plot is presented to facilitate interpretation of our species-level composition analyses.

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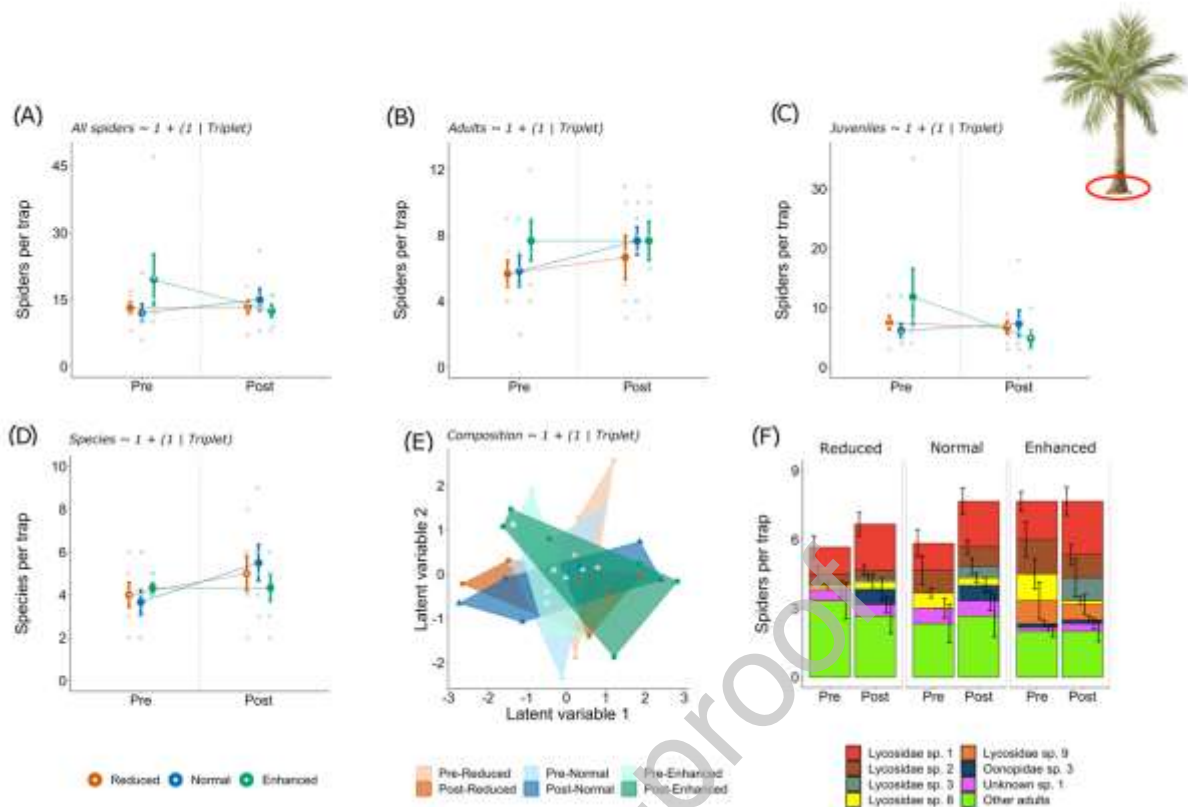


Fig. 4. Effects of the BEFTA-UVP treatments on the abundance of either all spiders (A), adults only (B), and juveniles only (C); spider species richness (D), and species-level composition (E & F) *on the ground*. In (A)-(D), posterior distributions from GLMMs tracked to their underlying datasets; circles and error bars indicate pre- and post-treatment means and associated standard errors (1 standard error from the mean), respectively (Reduced = Orange; Normal = Blue; Enhanced = Green); and white circles indicate raw per-palm data. In (E), points represent the posterior medians of the GLLVM that we used to visualise the findings of our species-level composition analyses. Polygons were drawn around medians representing samples from the same *Time* and *Treatment* groups. In (F), error bars indicate one standard error from the mean, and spider species are plotted as they are sequenced in the legend. The 7 most abundant species across samples are plotted separately from other adults. In (A)-(E), we indicate the optimal model for each analysis, as determined by LOO-IC (A-D) or backwards

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