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RESEARCH ARTICLE

Maintaining understory vegetation in oil palm plantations supports higher assassin bug numbers

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Abstract

1. The expansion of oil palm agriculture across Southeast Asia has caused significant biodiversity losses, with the reduction in habitat heterogeneity that accompanies the conversion of forest to oil palm being a major contributing factor. However, owing to their long commercial lifespan, oil palm plantations can support relatively high levels of vegetation complexity compared to annual crops. There is therefore potential for the implementation of management strategies to increase vegetation complexity and associated within-plantation habitat heterogeneity, enhancing species richness and associated ecosystem functioning within productive oil palm landscapes.
2. This study focusses on two species of assassin bugs *Cosmolestes picticeps and Sycanus dichotomus*, which are important agents of pest control within oil palm systems. Using a Before-After Control-Impact experimental manipulation in Sumatra, Indonesia, we tested the effect of three alternative herbicide spraying regimes and associated vegetation complexity treatments on assassin bug numbers. Our treatments encompass a range of current understory vegetation management practices used in oil palm plantations and include removing vegetation only in areas key to harvesting ("Normal"), removing all understory vegetation ("Reduced"), and allowing native vegetation to regrow naturally ("Enhanced"). We assessed both the long-term (18 months) and short-term (within 2 weeks) effects of our treatments following herbicide spraying.
3. Pre-treatment, we found high numbers of assassin bugs of both species in all plots. Long-term post-treatment, the abundance of both *C. picticeps* and *S. dichotomus*

declined in reduced understory plots, although this decline was only significant for *C. picticeps* (98%). In contrast, there were no significant differences in the post-treatment abundance of either species in the short-term.

4. These results suggest that the long-term decline in assassin bug abundance was likely to be caused by loss of vegetation, rather than any immediate effects of the herbicide spraying. Our findings have clear management implications as they demonstrate that maintaining vegetation in oil palm understories can benefit an important pest control agent.

KEYWORDS
assassin bugs (Reduviidae), biological control agents, habitat heterogeneity, integrated pest management (IPM), oil palm agroecology, tropical agriculture, understory vegetation

1 | INTRODUCTION

A growing human population and increasing per-capita demand for cheaper vegetable oil has led to the rapid expansion and intensification of vegetable oil-producing crops globally (Foley et al., 2005; Phalan et al., 2013; Wilcove & Koh, 2010). Due to its versatile uses and high productivity in comparison to other oil crops, palm oil has become the most widely produced vegetable oil worldwide, with the crop playing an increasingly important role in global food security and biofuel supply (Tan et al., 2009; Tilman et al., 2011). Nowhere is the growth in oil palm agriculture more evident than in Southeast Asia, a region that produces 89% of the world's palm oil, and where oil palm plantation area has increased almost fourfold since the turn of the 21st century (FAO, 2023). Indonesia, the world's leading producer of palm oil, is at the forefront of this production boom; here the palm oil industry has grown to become an invaluable contributor to the country's economic growth and national development (Gatto et al., 2015; Purnomo et al., 2020). However, as plantations are commonly established at the direct expense of biodiverse rainforest habitat, this expansion has also caused major deforestation and associated biodiversity loss in the region (Edwards et al., 2014; Fitzherbert et al., 2008; Gaveau et al., 2019; Turubanova et al., 2018). It is estimated that 54% of Indonesia's 14.6 million hectares of oil palm plantations have been directly established on previously forested land (Vijay et al., 2016).

While retaining remaining forest habitats is vital for supporting tropical biodiversity (Gibson et al., 2011; Phalan et al., 2011), an increased awareness of the negative impacts of palm oil production means there is growing pressure on the oil palm industry to develop sustainable management practices that improve biodiversity within plantations (Austin et al., 2017; Roundtable on Sustainable Palm Oil (RSPO), 2020). One of the major drivers of biodiversity loss resulting from habitat conversion is the simplification of vegetation, both in terms of overall species richness and structural complexity (Drescher et al., 2016; Foster et al., 2011). Although oil palm plantations are significantly less complex than forests, their long 25–30 year commercial lifespan and infrequent tillage (only occurring immediately pre-replanting) means they have the potential to develop considerably higher levels of understory vegetation complexity in comparison to annual vegetable oil-producing crops, such as soybean and rapeseed (Barcelos et al., 2015; Corley & Tinker, 2015; Luskin & Potts, 2011; Meijaard et al., 2018). For example, Luke, Purnomo, et al. (2019) found that mature oil palm plantations in Sumatra, Indonesia can support an understory vegetation layer consisting of 120 different fern and flowering plant species. An established understory may act as a nectar source for pollinators, a food source for herbivores, provide cover for predatory species and benefit temperature-sensitive taxa by buffering the ground-level microclimate (Hinsch, 2013; Luskin & Potts, 2011; Norman & Basri, 2010), potentially having a net positive impact on overall levels of biodiversity and ecosystem functioning.

Few studies have investigated the impacts on biodiversity of local-scale management practices that enhance understory complexity in oil palm plantations. Instead, the majority of research that has been carried out on management for heterogeneity within oil palm has focussed on increasing complexity at the landscape-scale, such as through retaining or replanting native trees in fragments (as in Lucey & Hill, 2012; Lucey et al., 2014; Teuscher et al., 2016; Zemp et al., 2019) or along rivers (as in Gray et al., 2015; Gray et al., 2016; Luke, Slade, et al., 2019; Mullin et al., 2020; Pashkevich et al., 2022; Williamson et al., 2020; Woodham et al., 2019). Given that guidance on local-scale management practices is already included in certain sustainability certification guidelines (such as those highlighted within Principle 7 of the Roundtable on Sustainable Palm Oil's Principles and Criteria [Roundtable on Sustainable Palm Oil (RSPO), 2020]), and that such practices are likely to be relatively easily and cheaply adapted to fit with future updated guidelines, it is of key importance that the outcomes of such practices are better understood. This is important not only to maximise yield, but to also minimise the costs of production to biodiversity and the wider environment.

The use of herbicides to control weeds, as a means to improve access for harvesting, as well as to maximise light, water and nutrient availability for the crop, is common practice in oil palm agriculture. This typically involves either targeted spraying around individual palms and along pathways, as is common practice in industrial plantations, or non-targeted blanket spraying, which is common in small-holding plantations (Corley & Tinker, 2015; Lee et al., 2014; Rutherford et al., 2011; Wibawa et al., 2007). In addition to impacting understory vegetation (e.g. Luke, Purnomo, et al. (2019) reported that understory floral species richness increased by as much as 43% in non-sprayed plantation plots), there is evidence that reduced herbicide application can lead to higher faunal abundance and diversity. This includes increased web-building spider abundance (Spear et al., 2018), ground-dwelling ant abundance (Hood et al., 2020), understory insect family richness (Darras et al., 2019), leopard cat activity (Hood et al., 2019) and more abundant and diverse belowground macrofauna (Ashton-Butt et al., 2018). With many of these taxa being directly associated with important ecosystem services, such as pest control, decomposition and nutrient cycling, reduced herbicide application also has the potential to enhance the level of ecosystem functioning within plantations. Therefore, reducing herbicide application within oil palm agriculture is not only a potentially practical and cost-effective way to increase plantation-wide understory vegetation heterogeneity, but also has the potential to positively impact wider biodiversity and alleviate some of the negative ecological impacts associated with agricultural expansion.

The Reduviidae (assassin bugs) are a large and biologically diverse family of predacious insects, with approximately 7000 species described globally (Gil-Santana et al., 2015). Many of these species play important roles as pest control agents within tropical agriculture, including in oil palm plantations, where, due to their polyphagous nature, they prey on a wide variety of insect pests, including the two main groups of oil palm defoliators present in Southeast Asia: nettle caterpillars (Lepidoptera: Limacodidae) and bagworms (Lepidoptera: Psychidae) (Ambrose, 2003; Cheong et al., 2010; Jamian et al., 2016; Wood & Kamarudin, 2019; Zulkefli et al., 2004). For many years, synthetic pesticides were used to control pest numbers in oil palm, however, their usage has now been largely phased out due to the wide-scale development of pest resistance, secondary poisoning of non-target organisms and potential risks to human health (Gill & Garg, 2014; Wilby & Thomas, 2002). Integrated pest management (IPM) has become an increasingly important alternative strategy for pest control in oil palm agriculture (Wood, 2002). IPM ultimately aims to complement, reduce, or replace the application of pesticides, through careful monitoring of pests, targeted control strategies, and enhanced natural biocontrol by key native predator species (Kogan, 1998; Toth, 2009), including assassin bugs. It is therefore important from both a conservation and yield perspective to understand how understory vegetation complexity within oil palm plantations affects assassin bugs.

In this paper, we investigate the impacts of three oil palm understory management strategies on two species of assassin bugs (*Cosmolestes picticeps* Stål, 1859 and *Sycanus dichotomus* Stål, 1866), both of which are generalist predators and widely cited as effective pest control agents within Southeast Asian agroecosystems (Norman et al., 1998; Sulaiman & Talip, 2021). To do this, we use a large-scale and long-term before-after control-impact (BACI) management experiment that has varied levels of herbicide applications with resultant effects on understory vegetation complexity in mature industrial oil palm. As applications of herbicides could affect assassin bug communities both long-term (through impacts on understory vegetation structure) and in the immediate short-term (through direct toxicity of herbicide exposure), we specifically investigate both long- and short-term effects, asking the following key questions:

1. What are the long-term (18 months after treatment) effects of varying understory vegetation treatments on the abundance of *Cosmolestes picticeps* and *Sycanus dichotomus*?
2. What are the short-term (within 2 weeks after treatment) effects of herbicide application on the abundance of *Cosmolestes picticeps* and *Sycanus dichotomus*?

2 | MATERIALS AND METHODS

2.1 | Study site

Data for this study were collected in industrial oil palm plantations owned and managed by PT Ivo Mas Tunggal, a subsidiary company of Golden Agri Resources (GAR), with technical input from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI) in Riau Province, Sumatra, Indonesia (N0 55.559, E101 11.619) (Figure 1). The area surrounding the plantations is dominated by oil palm agriculture and human infrastructure; the nearest intact forest (Siak Kecil Forest) is 60 km away, and the nearest degraded forest is 15 km away. The region has a wet tropical climate, with an average annual rainfall of 2350 mm (average monthly rainfall figures for the data collection period are shown in Figure S1).

The study was conducted across two neighbouring plantation estates (Ujung Tanjung and Kandista; Figure 1), both of which are RSPO certified, with GAR being an active member of the RSPO since 2005. The plantations were planted between 1988 and 1993 (see Table S1 for exact planting dates for each experimental plot), meaning oil palms were mature (aged 20–27 years) at the time of data collection in 2013, 2014 and 2015. Across the two estates, oil palms were planted in staggered rows at a density of 136 palms/ha, or approximately 8 m apart. The sites used in this study make up the Biodiversity and Ecosystem Function in Tropical Agriculture Understory Vegetation Project (BEFTA-UVP). The BEFTA-UVP is a long-term ecological experiment that investigates the effects of understory vegetation management in oil palm on biodiversity, ecosystem functioning and yield (Luke et al., 2020). Project sites consist of eighteen plots, arranged into six triplets. Each plot measures 150 × 150 m and is made up of a central 50 × 50 m core section and an outer buffer region. All plots are located at the ends of three neighbouring 300 × 1000 m plantation planting blocks, such that the middle plot in each triplet is 155 m from each of the outer plots within the triplet. Triplets are separated by at least 1 km (Figure 1). Each plot is established on flat ground, 10–30 m a.s.l., and is bordered by

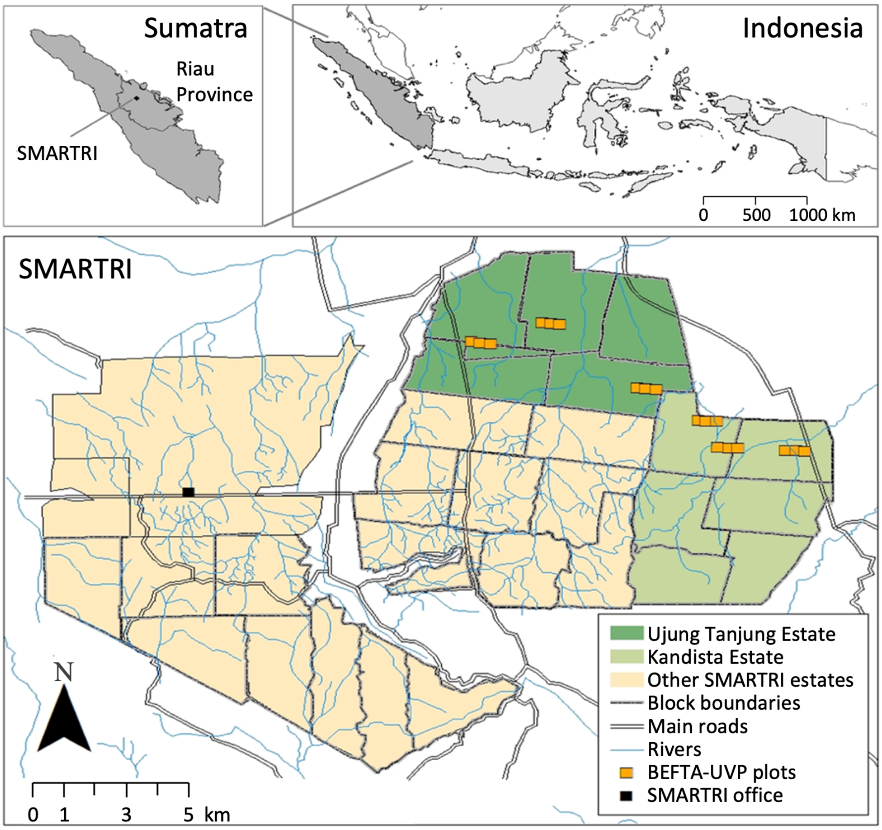

FIGURE 1 Location of BEFTA-UVP plots within SMARTRI estates (Riau, Sumatra, Indonesia). The 18 plots (orange squares) are arranged in triplets throughout the Ujung Tanjung, and Kandista Estates (coloured in green). The maps were created using ArcMap 10.5.1 (Environmental Systems Research Institute, 2017), and library "maps" in R statistical package (Brownrigg, 2016), with reference to maps produced by SMARTRI. [This figure has been adapted, with the permission of the authors, from a figure included in Luke et al., 2020].

an unpaved road and drainage ditch on one end, and by neighbouring oil palm on the remaining three sides. A stream runs through two of the plots.

Plots were established in October 2012, with understory management treatments implemented in February 2014. The three plots within each of the six triplets were randomly allocated to one of three understory treatments (hence, there were a total of six plots for each understory treatment) (Figure S2), representing the range of common management strategies used within industrial and smallholder oil palm plantations:

1. *Normal understory vegetation complexity (hereafter referred to as "Normal")*: This is standard industry practice used within the GAR estates and is how all plots were managed pre-treatment. It involves an intermediate level of herbicide spraying, with harvesting paths and circles (1.5 m radius areas around individual palm bases) being sprayed three to five times annually. All other vegetation elsewhere in the plots is allowed to regrow naturally, except for woody shrubs and young trees, which are removed manually.
2. *Reduced understory vegetation complexity (hereafter referred to as "Reduced")*: This is the highest intensity of understory vegetation management. It involves a high level of herbicide spraying, with all understory vegetation throughout the plots being sprayed three to five times annually, effectively killing all understory vegetation.
3. *Enhanced understory vegetation complexity (hereafter referred to as "Enhanced")*: This is the lowest intensity of understory vegetation management. It involves no herbicide spraying and only limited hand-cutting of woody vegetation to keep harvesting paths and areas around palm bases open and accessible. Cutting first took place 1 year after treatments started and was then carried out at the same frequency as herbicide application in the other treatments.

For full details of the effects of the BEFTA-UVP experiment set-up and effects of the treatments on understory plant communities, see Luke, Purnomo, et al. (2019) and Luke et al. (2020). Herbicides used included Glyphosate (Rollup 480 SL), Paraquat Dichloride (Rolixone 276 SL), metsulfuron-methyl (Erkafuron 20 WG), and Fluroxypyr (Starane 290 EC). Barring 6 days of geographically restricted pyrethroid based canopy fogging (see Pashkevich et al. (2022)) no insecticides were used in the plots throughout this study. Data collection was carried out during three separate time periods. To assess long-term effects of treatment, we collected pre-treatment data in September 2013 and post-treatment data in September 2015 in all eighteen plots. To assess short-term effects of treatment, we collected data in February 2014, just before (within 2 weeks, and hereafter referred to as 2014-Pre) and just after (within 2 weeks, and hereafter referred to as 2014-Post) herbicide application in each of the six Normal and six Reduced treatment plots (Figure S2). We did not survey the six Enhanced treatment plots at this time, as Enhanced and Normal plots were the same at this point, owing to not enough time passing for our Enhanced treatment to take effect.

2.2 | Assassin bug surveys

We surveyed adult Reduviidae of the species *Cosmolestes picticeps* and *Sycanus dichotomus* (the two most common/conspicuous assassin bug species found within the plantation sites according to local counterparts) along transects in the core of each study plot. Transect walks consisted of a recorder walking at a steady pace, counting any adult *C. picticeps* or *S. dichotomus* that were visible or flew up in front of the recorder (without deliberately disturbing vegetation) within a 5-m-sided cube of space in front of them. This meant that it was important that both species could be easily distinguished visually from each other and from other Reduviidae present within the plantations. This was only achievable for adult *C. picticeps* and *S. dichotomus* (Figure 2), meaning that earlier developmental stages (eggs and nymphs) were not recorded. Identifications were made following guidance from local counterparts. The transect was 200 m in length and followed the edge of the central 50 × 50 m core section within each plot, although we did not re-record areas of overlap at the end of the transect. Transects were walked between 9:00 and 17:00 and were not conducted when it was raining. Two repeat surveys of each plot were carried out on separate days in each sampling period, with total counts for each of the plots being averaged and rounded to the nearest whole number for analyses, except for 2014-Pre and 2014-Post, when time constraints meant that only one visit was possible per transect before and after treatment. Therefore, for our long-term analyses, the response variable was mean number of assassin bugs per 50 × 50 m transect over 2 days of sampling. For our short-term analyses, the response variable was number of assassin bugs per 50 × 50 m transect. We found that there was variation in counts between the two repeat surveys in each plot, but with a significant correlation between counts (Figure S3). By averaging surveys, we therefore reduced some of the stochastic variation related to individual surveys.

2.3 | Statistical analyses

We carried out all statistical analyses in R version 4.1.2 (R Core Team, 2021) using R Studio version 2021.09.1+372 (R Studio Team, 2021). For data wrangling and exploration, we used *readxl* (Wickham & Bryan, 2023), *tidyverse* (Wickham, 2019), *data.table* (Dowle & Srinivasan, 2023) and *plyr* (Wickham, 2016b), following the data exploration procedure outlined by Zuur et al. (2010). For data visualisation we used *cowplot* (Wilke, 2020), *lemon* (Edwards et al., 2022) and *ggplot2* (Wickham, 2016a).

We separately analysed the long-term and short-term impacts of understory vegetation treatment on *C. picticeps* and *S. dichotomus* using Bayesian generalised linear regression models (hereafter, GLMMs). We fitted GLMMs using *brms* (Bürkner, 2017) and the No-U-Turn sampler (NUTS) algorithm in Stan (Carpenter et al., 2017). We fitted five candidate models for each response: a parent model (*Time*Treatment*) and four derivative models (*Time* + *Treatment*, a *Time*-only model, a *Treatment*-only model and a null model), with '*Time*' being a categorical variable with two categories representing different sampling time points: after treatment in September 2015 (A) and before treatment in September 2013 (B), and '*treatment*' representing one of the three vegetation management types: Normal (N), Reduced (R) or Enhanced (E). We included *Triplet* as a random intercept effect in all models, to account for potential spatial autocorrelation, triplet-specific differences in environmental conditions and timing of sampling in our modelling. *Triplet* has six variables: UT_1, UT_2, UT_3, K_1, K_2 K_3, corresponding to the six triplets of BEFTA-UVP plots in Ujung Tanjung (UT) and Kandista (K) estates. As we were modelling count data, all models were fitted to Poisson distributions. We checked Poisson models for over-dispersion and found that they were not over dispersed (and therefore negative binomial models were not needed). We verified that negative binomial distributions did not improve model fits by calculating and comparing the leave-one-out cross-validation information criterion (LOOIC) of these models to that of our Poisson-distributed models. Owing to the high proportion of zeros within our dataset (particularly for *S. dichotomus*, with no individuals recorded in 58% of transects in the long-term data set and 42% of transects in the short-term data set), we also verified that zero-inflated models were not required.

We ran all GLMMs for 50,000 iterations using four chains and a thinning rate of 10. We discarded the first 8000 iterations as warm-up/burn-in samples and controlled the behaviour of the NUTS algorithm to decrease the number of divergent transitions (*adapt_delta* = 0.99). We fitted *normal* (0,10) priors on model intercepts, *normal* (0,10) priors on fixed effects, and *normal* (0,1) priors on the standard deviation of random effects. When testing negative binomial and zero-inflated models, we fitted *gamma* (0.01,0.01) priors on the negative binomial shape parameter and *beta* (0.1,0.1) priors on the zero-inflated parameter. We chose weakly informative

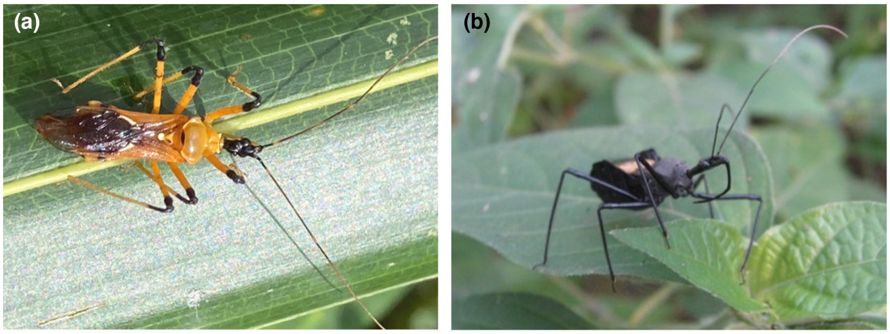

FIGURE 2 Photo of adult (a) *Cosmolestes picticeps* and (b) *Sycanus dichotomus*, taken within the BEFTA-UVP plots (credit Edgar Turner). *Cosmolestes picticeps* typically measures ~1.5 cm in body length and *Sycanus dichotomus* typically measures ~3 cm.

priors, to regulate the posterior distributions of our models such that they were kept within a reasonable range of values (i.e. they did not stray too far from the underlying datasets). For details of each of the models fitted during analyses see Table S2.

We determined that mixing was sufficient by inspecting Markov chain Monte Carlo (MCMC) trace plots, ensuring that Rhat values were <1.1, the ratio of effect sample size to total sample size was >0.1, and no autocorrelation was present within the MCMC chains (Muth et al., 2018). We validated models by verifying that no patterns were present when Pearson residuals were plotted against fitted values, included covariates, and random effect levels. We then used posterior predictive checks to ensure that attributes of data that were simulated from each model accurately reflected the real dataset from which each model was generated. For example model validation plots see Figures S4–S9. Model validation and posterior predictive checks required *bayesplot* (Gabry & Mahr, 2022) and *tidybayes* (Kay, 2023).

After generating and validating all candidate models, we took an information criterion approach to choose a model of best fit. This model selection process involved calculating and comparing each model's LOOIC. We selected the model with the lowest LOOIC as the optimal model (i.e. a model that explained the most variation in the data with the fewest parameters), unless the standard errors of the LOOIC overlapped with that of another candidate model, in which case we selected the model with fewer parameters as the optimal model (Gabry et al., 2019). If the null model was not the optimal model, we report model estimates and 95% credible intervals for fixed effect parameters, and used *emmeans* (Lenth et al., 2018) to conduct post-hoc analyses by computing estimated marginal means for each factor level and comparing these in a pairwise fashion. We concluded that factor levels were meaningfully different if the 95% highest posterior density interval of the median point estimate calculated from our comparisons did not overlap with zero.

3 | RESULTS

Assassin bugs were relatively abundant throughout the plots, with a total of 622 individuals recorded across the three sampling periods (September 2013, February 2014, and September 2015), representing an average density of 104 assassin bugs recorded per hectare. Across the study, *C. picticeps* was far more abundant (542 individuals, and 87% of total abundance) than *S. dichotomus* (80 individuals, and 13% of total abundance).

3.1 | Long-term effects of understory vegetation treatments

Four hundred and thirty-six assassin bugs (394 *C. picticeps* and 42 *S. dichotomus*) were recorded for use in long-term treatment analyses; 264 (239 *C. picticeps* and 25 *S. dichotomus*) in 2013 and 172 (155 *C. picticeps* and 17 *S. dichotomus*) in 2015. Per-plot abundance for *C. picticeps* was significantly affected by the interaction between sampling period and treatment type, with the maximum model (*Cosmolestes Picticeps* ~ *Time***Treatment* + (1|*Triplet*)) being the optimal model ($R^2 = 52.1 \pm 5.7\%$; Figure 3a). Post-hoc analyses showed that there were no differences in pre- and post-treatment abundances of *C. picticeps* for Enhanced (Model estimate (95% credible interval) for pre-Enhanced = 5.669 (3.592–8.488); for post-Enhanced = 6.458 (4.206–9.765)) and Normal (Model estimate (95% credible interval) for pre-Normal = 7.435 (4.886–10.884); for post-Normal = 6.162 (3.993–9.238)) treatments. However, for the Reduced treatment (Model estimate (95% credible interval) for pre-Reduced = 7.242 (4.681–10.832); for post-Reduced = 0.116 (0.005–0.619)), per-plot abundance of *C. picticeps* was 98% lower in 2015 than in 2013 (average abundances of 1 and 45 respectively, across the six plots; Figure 3e). In contrast, for *S. dichotomus* we found no significant effects of understory vegetation treatment, season, or the interaction between these variables, with the Null model being the optimal model ($R^2 = 6.3 \pm 6.3\%$; Figure 3b). This was despite per plot abundances of *S. dichotomus* in the Reduced treatment plots being 86% lower in 2015 than in 2013 (average abundances of 1 and 7, respectively, across the six plots; Figure 3e).

3.2 | Short-term effects of understory vegetation treatment

One hundred and eighty-six individuals (148 *C. picticeps* & 38 *S. dichotomus*) were recorded in the 2014 season: 114 (91 *C. picticeps* & 23 *S. dichotomus*) immediately before treatment application, and 72 (57 *C. picticeps* & 15 *S. dichotomus*) immediately after. For the immediate pre and post dataset, we found no effects of understory vegetation treatment, season or the interaction of these variables on either *C. picticeps* or *S. dichotomus*, as the null model was the optimal model for both species ($R^2 = 10.1 \pm 8.1\%$ and $R^2 = 6.5 \pm 6.3\%$; Figure 4).

4 | DISCUSSION

In this study, we tested whether different levels of understory vegetation management ("Normal"—herbicide spraying to remove understory vegetation only in areas key to harvesting, "Reduced"—spraying all understory vegetation, and "Enhanced"—no spraying and allowing understory vegetation to regrow naturally) affected two species of assassin bug (*C. picticeps* and *S. dichotomus*) in mature oil palm plantations. We found that assassin bugs were common across our plots, with 622 individuals recorded throughout our study. *C. picticeps* was found to be far more abundant than *S. dichotomus* within the plots sampled (respective ratio 6.8: 1); this matches well with figures presented by Jamian et al. (2016), the only other study that we could find to have recorded numbers of both species within oil palm agriculture. This is potentially due to *S. dichotomus* being considerably larger than *C. picticeps*, with large-bodied insects often being rarer

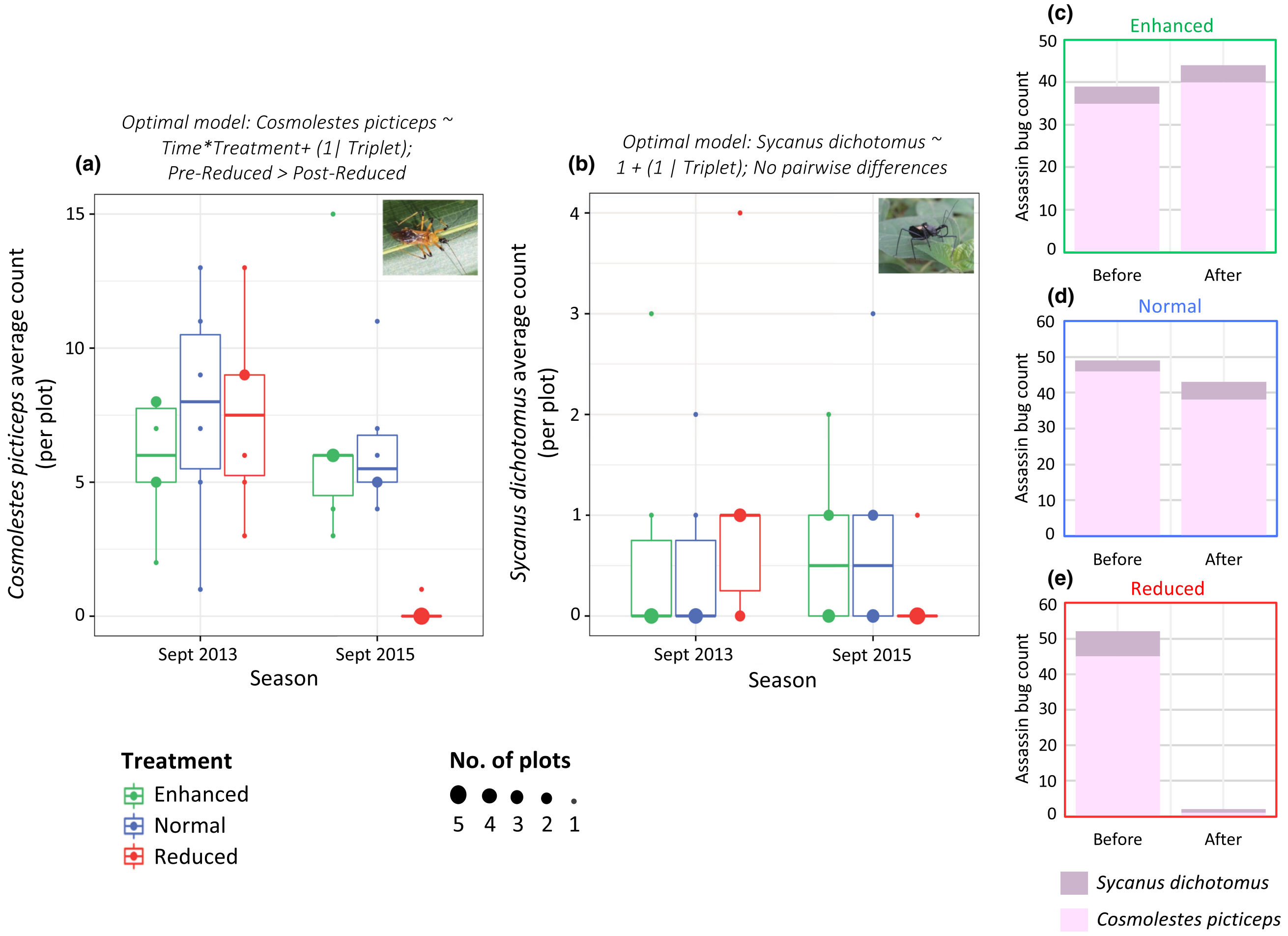

FIGURE 3 Average per-plot abundance of: (a) *Cosmolestes picticeps* & (b) *Sycanus dichotomus* both before (6 months pre-treatment) and after (18 months post-treatment) treatment in Enhanced, Normal and Reduced plots. Boxplots display median and interquartile ranges (IQR), and whiskers incorporate data that are 1.5*IQR. The mean abundance in each of the 18 plots (6 replicate plots per treatment) is represented by a dot; the size of the dot is determined by how many plots share the same abundance. Stacked bar graphs (c–e) illustrate total number of *Cosmolestes picticeps* and *Sycanus dichotomus* before and after treatment in each of the three treatment types.

than smaller-bodied insects in ecosystems (Siemann et al., 1996). We found a significant negative long-term effect of reduced understory vegetation on *C. picticeps* (per-plot abundance in reduced vegetation treatments was 98% lower 18 months post-treatment than it was pre-treatment), but not for *S. dichotomus* numbers, although there was also a trend for *S. dichotomus* abundance to decline (86% decline over the same period). In contrast, there was no significant observed effect of the enhanced vegetation treatment (where no herbicide was applied) on abundance of either species over the same time period. We also recorded no significant changes in assassin bug numbers immediately post treatment in 2014, indicating that there were no detectable immediate effects of herbicide spraying.

4.1 | Long-term effects of understory vegetation treatment

The strong declines we observed in the abundance of *C. picticeps* in reduced vegetation treatment plots, but not normal or enhanced vegetation plots, suggests that understory vegetation plays a vital role in the survival of this species. This may be a direct result of the structure provided by an established understory, as the leaves and stems of herbaceous plants often provide the primary substrate for assassin bug oviposition (Ambrose & Livingstone, 1989). Furthermore, it is possible that eggs laid onto vegetation before herbicide application may have experienced reduced hatching success if plants died before nymphs emerged, with long-term effects on adult numbers. The lower abundance of *C. picticeps* in reduced vegetation plots may also be linked to the fact that understory vegetation likely supplies a vital food source for assassin bugs, by providing resources for small invertebrate prey, as shown by previous findings from the BEFTA-UVP (Ashton-Butt et al., 2018; Hood et al., 2020; Spear et al., 2018), as well as work carried out by Darras et al. (2019) and Teuscher et al. (2016), who reported that a more diverse and structurally complex oil palm understory promoted higher invertebrate abundance and richness. The cover provided by understory vegetation may also be a factor, as it can act as a refuge from predation, as well as creating more favourable microclimatic conditions

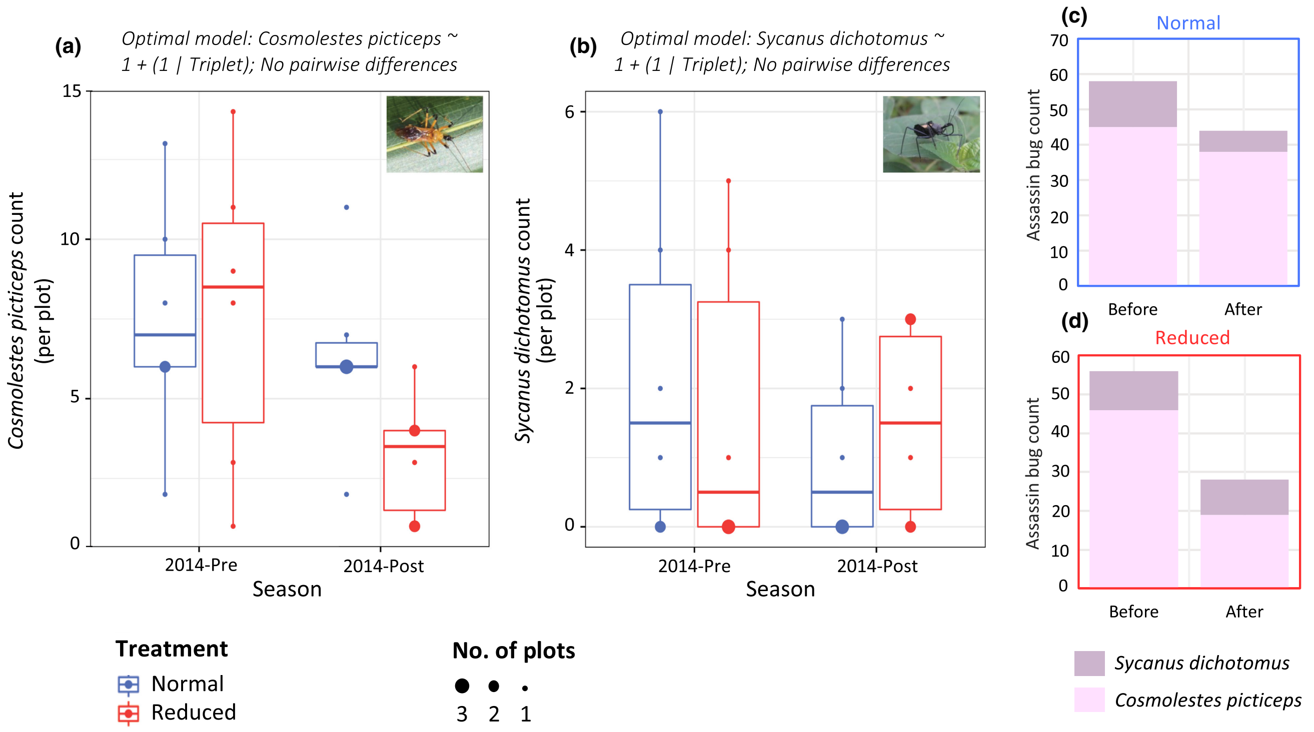

FIGURE 4 Per-plot abundance of: (a) *Cosmolestes picticeps* & (b) *Sycanus dichotomus* for both immediately pre- and immediately post-treatment in Normal and Reduced plots. Boxplots display median and interquartile ranges (IQR), and whiskers incorporate data that are 1.5*IQR. The abundance in the 12 plots (6 replicate plots per treatment) is represented by a dot; the size of the dot is determined by how many plots share the same abundance. Stacked bar graphs (c and d) illustrate total number of *Cosmolestes picticeps* and *Sycanus dichotomus* before and after treatment in the two treatment types.

for assassin bugs, such as cooler temperatures and higher humidity. Finally, some assassin bug species, including *C. picticeps*, are known to supplement their diet with extrafloral nectar (Jamian et al., 2016); therefore, access to a more diverse floral understory might also result in higher assassin bug numbers. Overall, it is likely that a combination of mechanisms drive *C. picticeps* abundance within oil palm plantations, and that by removing understory vegetation, assassin bug survival, reproductive and immigration rates decrease, while relocation rates to more-favourable areas increase.

Although the abundance of *C. picticeps* is significantly associated with the presence of understory vegetation, there was no clear observable difference between *C. picticeps* numbers in normal and enhanced vegetation plots. This could be because normal vegetation plots only receive herbicide along access paths and in the area surrounding palms, and indicates that the levels of understory maintained in normal plots are sufficient to support assassin bugs at abundances similar to those in enhanced plots. This suggests that current herbicide management regimes in GAR plantations are not having a negative impact on assassin bug numbers. The lack of difference in understory vegetation complexity between normal and enhanced plots has also been recorded in other BEFTA-UVP studies. Indeed, Luke, Purnomo, et al. (2019) found that the species richness and biomass of understory vegetation did not differ between the two treatment types more than a year after treatment, while studies in the system on different invertebrate taxa that recorded reduced abundance in reduced vegetation plots (Hood et al., 2020; Spear et al., 2018), have also reported a lack of difference between normal and enhanced vegetation treatments.

The lack of a significant difference in *S. dichotomus* abundance between treatments is most likely related to the lower overall numbers of *S. dichotomus* observed throughout our plots, making it harder to detect any significant effects of treatment. If true, this indicates that many of the factors that influenced the reduction in *C. picticeps* abundance are also likely to impact *S. dichotomus*. Indeed, previous research indicates that the ability to access, and preference for different within-plantation vegetation stratum is similar for both species (Jamian et al., 2016; Norman & Basri, 2010). However, it could also be that *S. dichotomus*, being considerably larger than *C. picticeps*, is more dispersive and therefore less affected by the spatial scale at which treatments were applied (150 × 150 m plots). Its size also means that its surface area to volume ratio is lower, potentially allowing it to be more robust to impacts mediated by changes in microclimate, such as increased aridity (Kühsel et al., 2017).

4.2 | Short-term effects of understory vegetation treatment

There was no clear short-term effect of spraying herbicides on assassin bug numbers, suggesting that the herbicide spraying itself does not have an immediate effect on assassin bugs. This again indicates that factors associated with changes in understory vegetation complexity are more likely to be driving differences in assassin bug numbers in oil palm plantations. As we sampled very soon after spraying in the Reduced vegetation plots, much of the vegetation, although dead or dying, was still present, providing some benefit for foraging and as refuge from predation and microclimate. Similarly, any prey insects attracted by this vegetation may still have been present. However, as adult assassin bugs readily fly when disturbed, it is likely that many may have avoided direct contact with herbicides during spraying, potentially explaining this lack of effect. Furthermore, as it was only adults that were recorded, any potential toxic impact of herbicide application on flightless nymphs would not have been picked up in our short-term abundance figures. It must also be noted that due to logistical constraints, we were unable to carry out two surveys pre and post treatment in 2014, so it is possible that the lower numbers in this analysis could have reduced the chance of detecting any differences. Indeed, *C. picticeps* numbers were lower immediately post-treatment in the Reduced plots, although this difference was not detected statistically in our modelling.

4.3 | Management implications

The results of this study have several management implications. As both *C. picticeps* and *S. dichotomus* are known to be effective predators of several major oil palm pests, the relatively high abundance we recorded indicates that both species are potentially important pest control agents in the plantations we studied, reflecting findings in oil palm systems in other parts of the tropics (Ahmad et al., 2020; Jamian et al., 2016; Norman & Basri, 2010). Given the drop in assassin bug numbers we detected within reduced vegetation treatment plots, it is our advice that the blanket spraying of herbicides in oil palm plantations should be actively avoided. We instead suggest that plantations in which blanket spraying is standard practice (e.g. in many smallholdings, Lee et al., 2014), should switch management practice to a targeted herbicide approach as a matter of priority. There is also a growing body of research that highlights the potential associated risk of herbicide application to human health (Abdul et al., 2021; Kim & Kim, 2020; Myers et al., 2016), so such a reduction in application is also likely to come with additional benefits for growers. Our findings also suggest that in order to enhance assassin bug numbers in oil palm, the implementation of more proactive management strategies, such as the planting of beneficial understory species, as highlighted in Jamian et al. (2016), are required. Owing to the role of assassin bugs as pest control agents (Ambrose, 2003), it is likely that if understory vegetation is maintained and assassin bug numbers are boosted, it could also result in enhanced pest control services and lower herbivory, with potential benefits to palm oil yield. This is in line with a growing pool of evidence that highlights the importance of floral diversity and structural complexity of vegetation for increasing the abundance of invertebrate predators and parasitoids of crop pests (Chaplin-Kramer et al., 2011; Landis et al., 2000; Langellotto & Denno, 2004; Wratten et al., 2002). It is therefore our recommendation that clear directives concerning reducing herbicide usage within oil palm crop matrices (either through limiting the frequency of general application or limiting application to distinct zones, i.e. access pathways) should be integrated within major certification and sustainability guidelines. For example, under Principle 7 of the Roundtable on Sustainable Palm Oil's Principles and Criteria for the Production of Sustainable Palm (Roundtable on Sustainable Palm Oil (RSPO), 2020), a new subpoint within section 7.1 (Section criteria: Pests, diseases, weeds and invasive introduced species are effectively managed using appropriate integrated pest management techniques) could be created. This would provide guidance on levels of herbicide usage, as well as highlight the importance of maintaining understory vegetation in boosting pest control agents within oil palm agriculture, citing this study as well as others published from the BEFTA-UV Project (e.g. Hood et al., 2019, 2020; Spear et al., 2018).

Our findings highlight the importance of understory vegetation for supporting biodiversity in oil palm, as well as potential associated pest control benefits. Given that several ecological factors are likely driving these results, further research that aims to provide a clearer understanding of the weighting of such factors could help with directing future management strategy. More work is also required urgently to assess the practicality of implementing such lower intensity management across oil palm plantations, particularly the long-term impacts on pest numbers and yield. As herbicide applications can constitute a significant component of the costs of oil palm management (Levin et al., 2012), it is also possible that such a change could benefit profitability, while reducing any negative external effects of chemical applications on human health. With oil palm now grown on over 28 million hectares globally (FAO, 2023), these relatively simple changes to management practices have the potential to have widespread ecological benefits.

AUTHOR CONTRIBUTIONS

Our study brings together authors from multiple countries, including researchers based in the country where the study was carried out. Jake Stone led statistical analyses (with assistance from Michael D. Pashkevich) and writing of the manuscript. Amelia S. C. Hood created the original template for code used in statistical analysis. Jean-Pierre Caliman, William A. Foster, Jake L. Snaddon, Sarah H. Luke and Edgar C. Tuner designed the study. Anak Agung Ketut Aryawan, Mohammad Naim, Pujianto, Dedi Purnomo, Suhardi, Ribka Sionita Tarigan, Tuani Dzulfikar Siguga Rambe and Rudy Harto Widodo contributed to the sampling design and experimental protocols. Andreas Dwi Advento and Edgar C. Turner collected field data. All authors reviewed and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

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.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

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

Figure S1. Average monthly rainfall in millimetres (blue line) across the Kandista and Ujung Tanjung plantation estates, over the course of the study. Vertical green bars highlight the three sampling periods in which assassin bugs were recorded and the red line indicates when experimental treatments were implemented.

Figure S2. Plot set up of the BEFTA Understory Vegetation Project. Each panel (A and B) represents a triplet of experimental plots.

Figure S3. Correlation plots to determine the relationship between repeat surveys of *Cosmolestes picticeps* and *Sycanus dichotomus*, with first sample count on *x*-axis and second sample count on *y*-axis.

Figure S4. Example of density (left) and trace (right) plots to determine that mixing of MCMC chains was good.

Figure S5. Example visualisation of the “Eff. Sample” value, used to estimate the effective sample size.

Figure S6. Example visualisation to determine that there was no autocorrelation of the MCMC chains in our modelling.

Figure S7. Example diagnostic plots created during model validation.

Figure S8. Example posterior predictive check plots created during model validation.

Figure S9. Example posterior predictive check plots created during model validation.

Table S1. Details of the BEFTA-UVP plots at which data were collected, including- estate name, triplet number, plot name, understory vegetation treatment (randomly allocated to the plot), and date (data provided by SMARTRI) that palms were planted within each plot.

Table S2. Models fitted to assess the effects of the BEFTA-UVP treatments on assassin bug numbers.

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