



Removing understory vegetation in oil palm agroforestry reduces ground-foraging ant abundance but not species richness

Amelia S.C. Hood^{a,*}, Andreas D. Advento^b, Jake Stone^a, Tom M. Fayle^{c,d},
Alice L.M. Fairnie^e, Helen S. Waters^a, William A. Foster^a, Jake L. Snaddon^f,
Sudharto Ps^b, Jean-Pierre Caliman^b, Mohammad Naim^b, Edgar C. Turner^a

^aDepartment of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

^bSinar Mas Agro Resources and Technology Research Institute (SMARTRI), Jalan Teuku Umar, No. 19, Pekanbaru 28112, Riau, Indonesia

^cBiology Centre of the Czech Academy of Sciences, Institute of Entomology, Branisovska 1160/31, 370 05 Ceske Budejovice, Czechia

^dInstitute for Tropical Biology and Conservation, Universiti Malaysia Sabah, 88400 Kota Kinabalu, Sabah, Malaysia

^eSainsbury Laboratory, University of Cambridge, 47 Bateman St, Cambridge CB2 1LR, UK

^fSchool of Geography and Environmental Science, University of Southampton, Southampton, UK

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Abstract

Ants are known to provide valuable ecosystem services in agricultural landscapes, including oil palm plantations. Their communities are less diverse and more uneven in oil palm compared with forest, and this may increase their vulnerability to disturbance. This study quantifies ant communities in oil palm agroforestry and experimentally tests their robustness to a common-practice high-disturbance management intervention: removing understory vegetation.

Fieldwork was based at the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Understory Vegetation Project in Sumatra, Indonesia, where three treatments varying in their degree of understory vegetation management were established in 2014: (1) widespread herbicide was applied removing all understory vegetation (Reduced); (2) herbicide was applied to the harvesting paths and circles, and other vegetation was allowed to grow (Normal – control); (3) no herbicide was applied (Enhanced). We measured ground-foraging ant communities before and after the treatments were implemented, using pitfall traps over 324 trap-nights (a trap-night is one trap set for one night). We investigated how ant abundance, species richness, species evenness, beta diversity, and community composition differed between the treatments.

We found 3507 ants across 68 species or morphospecies. Seven of these were highly abundant and accounted for 78% of individuals. Post-treatment ant abundance was lower in the reduced treatment (mean per plot: 84) than in the normal (159) and enhanced (131) treatments, which did not differ from each other. Species richness, species evenness, beta diversity and community composition were not affected by the vegetation treatments.

We recommend that oil palm growers maintain understory vegetation in oil palm plantations to support ground-foraging ants. Though not tested here, this may also improve ant-mediated ecosystem services, such as pest control, seed dispersal, nutrient redistribution, and the maintenance of soil health. This study demonstrates that enhancing habitat complexity through management practices can support biodiversity in monocrop landscapes.

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*Corresponding author.

E-mail address: ah684@cam.ac.uk (A.S.C. Hood).

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Introduction

Globally, the area of agricultural land is approaching the total area that can produce food (Lambin & Meyfroidt, 2011; Rizvi, Pagnutti, Fraser, Bauch, & Anand, 2018), but food demands continue to increase (Keating, Herrero, Carberry, Gardner, & Cole, 2014). Sustainably intensifying existing landscapes is one of the foremost challenges of our time (Godfray & Garnett, 2014). Oil palm plantations are one such landscape. They yield palm oil, which is the most produced vegetable oil in the world; seventy-six million metric tons were produced in 2019, comprising 37% of all global vegetable oil production (United States Department of Agriculture (USDA), 2019). The rapid expansion of oil palm plantations into rainforest and peatlands in the tropics (Stibig, Achard, Carboni, Raši, & Miettinen, 2014; Wicke, Sikkema, Dornburg, & Faaij, 2011) has been associated with acute losses of biodiversity (Foster et al., 2011; Koh & Wilcove, 2008) and increases in pollution, including carbon emissions (Koh, Miettinen, Liew, & Ghazoul, 2011; Reijnders & Huijbregts, 2008). One of the drivers of this biodiversity loss is the reduced structural complexity of oil palm plantations compared with the forest that it has replaced (Zemp et al., 2019). Therefore, altering management strategies to increase complexity may help to mitigate the negative impacts of producing homogenous crops such as oil palm.

Although oil palm plantations are structurally simpler than forests, they are much more complex than other major oil crops, such as rapeseed and sunflower, and can support an understorey vegetation structure that is several metres high (Luke, Advento, et al., 2019) with over a hundred different plant species (Luke, Purnomo, et al., 2019). In addition to increasing structural complexity and plant diversity, understorey vegetation can buffer the microclimate (Luke, Advento, et al., 2019), which reduces the temperature extremes that are recorded in oil palm plantations compared with forest (Hardwick et al., 2015) and potentially favours temperature-sensitive taxa. Experimental manipulations have shown that reducing understorey vegetation complexity in oil palm plantations decreases Leopard Cat activity (Hood et al., 2019), bird species richness (Nájera & Simionetti, 2010), understorey spider abundance (Spear et al., 2018), understorey insect family richness (Darras et al., 2019), and belowground macrofauna abundance (Ashton-Butt et al., 2018) and order richness (Darras et al., 2019). Many of these taxa are associated with valuable ecosystem services in oil palm plantations, such as pest control (Koh, 2008; Verwilghen, 2015) and maintaining soil health (Ashton-Butt et al., 2018; Tuma et al., 2019). Despite these benefits, growers often spray herbicide liberally and remove all

of the understorey vegetation (Corley & Tinker, 2015; Wibawa, Mohamad, Omar, & Juraimi, 2007).

Understanding the impact of understorey vegetation management on ant communities in oil palm is particularly important because ants mediate many ecosystem functions (Elizalde et al., 2020). In oil palm plantations, they are the most abundant invertebrates in the soil, leaf-litter, epiphytes, and canopy (Ashraf et al. 2018; Carron et al. 2015; Ashton-Butt et al. 2018; Ganser et al. 2017). Their high abundance is a key feature that makes them so influential; experimental suppressions of ants in other tropical systems have shown that they drive soil properties (Evans, Dawes, Ward, & Lo, 2011), are the primary agents of resource removal (Griffiths et al., 2018), and regulate ecosystem functions including decomposition and herbivory through high rates of insect predation (Parr, Eggleton, Davies, Evans, & Holdsworth, 2016). Furthermore, ant suppression experiments in tropical agricultural systems have shown that there is little ecological redundancy for ant-mediated functions, and suppressing them reduces crop yield by 30–50% (Evans et al., 2011; Gras et al., 2016; Wielgoss et al., 2014). Within oil palm plantations, ants are the most important predators of insect pests (Nurdiansyah, Denmead, Clough, Wiegand, & Tscharnke, 2016), which often devastate crops and can result in almost complete loss of yield (Turner & Hinsch, 2018). Understanding the impact of understorey vegetation management on ant communities is therefore highly important from a yield perspective as well as a conservation one. One study has shown that below-ground ant abundance is reduced when understorey vegetation is removed (Ashton-Butt et al., 2018), but the effect of understorey vegetation management on ant species richness, ant community composition, and above-ground ant abundance has not yet been investigated.

Ant communities in oil palm plantations may be particularly vulnerable to disturbance, such as the removal of understorey vegetation, as they are often less abundant and have a lower diversity and evenness in oil palm than in the forest that the oil palm has replaced (Fayle et al., 2010; Turner & Foster, 2009; Wang & Foster, 2015). Studies show average reductions in species richness of over 60% between forest and oil palm (Fayle et al., 2010). Community composition also differs; oil palm plantations are characterised by having a few highly dominant species, which are often tramp or invasive ants (Pfeiffer, Cheng Tuck, & Chong Lay, 2008, Fayle et al., 2010). Though its effect in oil palm has not been tested, high species unevenness is associated with pest outbreaks in agriculture (Crowder, Northfield, Strand, & Snyder, 2010) and with greater vulnerability to impacts of environmental stress on ecosystem functioning (Wittebolle et al., 2009). Indeed, comparisons of

ant-mediated ecosystem services in forest and oil palm have recorded reduced rates of functioning; invertebrate predation rates are 70% lower in oil palm compared with neighbouring forest (Nurdiansyah et al., 2016), and rates of resource removal are also reduced (Gray, Lewis, Chung, & Fayle, 2015). Therefore, although ants provide valuable services in the oil palm landscape, management interventions aimed at increasing the abundance and diversity of their diminished populations may also improve the magnitude and resilience of the services that they provide. Furthermore, understanding the impact of management interventions on ants may provide an insight into the responses of other groups, as ground-foraging ants are good indicators of other animals in this system (Edwards et al., 2014).

This study will address the following questions:

1. What is the abundance and species composition of ground-dwelling ants in mature oil palm plantations?
2. What is the impact of varying understory management practices on ant abundance, species richness, species evenness, beta diversity, and community composition?

Materials and methods

Study sites

This research was conducted as part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme in Riau, Sumatra, Indonesia (0° 56' 0" N, 101° 18' 0" E). Oil palm estates in the BEFTA area are owned and managed by PT Ivo Mas Tunggal, a subsidiary company of Golden Agri Resources (GAR), with technical advice from Sinar Mas Agro Resources and Technology Research Institute (SMARTRI, the research and development centre of GAR). Historically, the area was lowland rainforest that was logged in the 1970s and converted to oil palm in 1985–1995. The region is managed as a large-scale industrial oil palm plantation; there are few other crops in the area and the nearest intact forest is 60 km away. Oil palm has been planted at a density of 147 palms/ha in staggered rows.

The BEFTA Understory Vegetation Project (BEFTA UVP) is a large-scale, long-term ecological experiment within the BEFTA Programme that is investigating the effects of understory vegetation management on biodiversity, ecosystem functioning, and yield in mature first-generation oil palm plantations (planted 1988–1993). Three experimental treatments that varied in their level of herbicide application, and therefore understory vegetation complexity, were implemented in February 2014. The treatments were assigned in a randomised complete block design with six replicates. Plots were 150 m × 150 m. Within a block, plots were separated from each other by 150 m, and blocks were at least one kilometre apart (see Luke, Advento, et al. 2019 for full information on study site and experimental design).

The three experimental treatments were as follows:

1. **Reduced complexity (Reduced):** All understory vegetation was removed by spraying herbicide.
2. **Normal complexity (Normal – control):** Understory vegetation was removed from the harvesting paths and harvesting circles using herbicide. Harvesting paths were approximately 1 m wide; they ran parallel to every second row of palms with one perpendicular path connecting them in each plot. The harvesting circle was an area around the base of each oil palm tree approximately 1.5 m in radius. Large woody vegetation was removed from all over the plots manually and all other vegetation was allowed to grow. This is how the plots were managed pre-treatment and is standard industry practice in the study area.
3. **Enhanced complexity (Enhanced):** No herbicide was used. Large woody vegetation was removed manually, and all other vegetation was allowed to grow.

The treatments have affected the understory vegetation and microclimate. The normal and enhanced plots have taller vegetation, greater plant biomass, higher plant species richness, and lower afternoon soil temperatures than the reduced plots (Luke, Advento, et al., 2019; Luke, Purnomo, et al., 2019). The plant species and the percentage cover of bare ground differs between all treatments (Luke, Advento, et al., 2019; Luke, Purnomo, et al., 2019). See the publications listed in Luke, Advento, et al., 2019 for differences in fauna and ecosystem functioning.

Ant collection and identification

Data collection followed a before–after-control-impact (BACI) design with the three treatment levels and two time-points. Pre-treatment data were collected in March–April 2013, and post-treatment data were collected in September 2014, seven months after the treatments were implemented. We set three pitfall traps in each plot. Traps were 50 m apart, arranged in an equilateral triangle that was centred in each plot. Each trap was active for three days. This amounted to 108 traps over 324 trap-nights. Traps consisted of circular 20 cm diameter funnels, leading to a pot of 75% alcohol (Fig. S1). This shape and size are ideal for sampling ants (Abensperg-Traun & Steven, 1995; Ahmed & Petrovskii, 2019), and we used ethanol as a killing agent because it does not attract or repel ants (Greenslade & Greenslade, 1971). Although a combination of Winkler litter sifting and pitfall trapping maximises the number of ant species collected (Donat Agosti & Alonso, 2000), we only used pitfall traps in this study, as Winkler traps provide very few additional species in habitats with poor litter cover (Lopes & Vasconcelos, 2008), such as oil palm plantations (Philip, Fayle, & Yusah, 2018).

Upon collection of the traps, we sieved the contents through a fine sieve with 1 mm mesh (Fig. S1) and stored the invertebrates. All worker ants were identified to genus using two keys (Fayle, Yusah, & Hashimoto, 2014; Schmidt & Shattuck, 2014). They were further identified to morpho-species or, where possible, to species using antweb (antweb.

org). For brevity, we will henceforth use the term species to include both fully-identified species and morphospecies. Reproductives (i.e. queens and males) were excluded from these analyses, as resources for their precise identification are limited and their swarming behaviour could create an unrepresentative count of species density. One species (*Pheidole* sp.1) may be a multispecies complex, as workers varied in size and colouration; there were no clear divisions along which to assign different species, so all individuals in this group were combined into a single morphospecies. A morphoseries of the identified specimens are housed at the Indonesian Institute of Sciences (LIPI) and all other specimens are stored at SMARTRI.

Statistical analysis

We analysed data in the software package R version 3.5.1 (R Core Team, 2018) with R Studio version 1.1.456 (RStudio Team, 2016), package *tidyverse* (Wickham, 2017) for data wrangling and plotting, and package *cowplot* (Wilke, 2019) for compiling plots. Some ant species can forage distances greater than 50 m and regularly forage to 40 m (Merkle & Wehner, 2010). We therefore combined the three pitfall traps in each plot when analysing these data, as their close proximity meant that they were not independent sample points. Three post-treatment pitfall traps were excluded from the analysis owing to loss or damage: one from each of two Reduced plots and one from a Normal plot. Due to the difficulties with averaging values such as species richness by plot, we analysed the results with this slightly uneven sample size. As this was at most 10% fewer traps at any one time, it is unlikely that including these traps would have altered our findings. To assess the completeness of sampling, we created a species accumulation curve for each vegetation management treatment pre- and post-treatment using the rarefaction method with the R package *vegan* (Oksanen et al., 2018). We used an incidence-based metric (B_{sim}) to calculate beta-diversity using the package *betapart* (Baselga, Orme, Villegier, Bortoli, & Leprieur, 2018). This metric provides one of the most robust measures of species turnover (Koleff, Gaston, & Lennon, 2003).

We ran a series of generalised linear mixed-effect models (GLMMs) to determine the effect of the interaction between vegetation management (categorical with three levels) and time (categorical with two levels) on ant abundance, species richness, and species evenness. For species evenness, we used the package *benthos* (Walvoort, 2019) to calculate Hurlbert's Probability of Interspecific Encounter, which gives the probability, bounded between zero (perfectly uneven) and one (perfectly even), that two individuals selected at random (without replacement) from a sample would belong to different species. We used a Poisson distribution when modelling species richness and a negative-binomial distribution when modelling abundance as the Poisson distributed model was overdispersed. We used a

beta distribution when modelling species evenness. We included the random effect block identity (categorical with six levels) in all models to account for spatial dependency. We ran GLMMs using Bayesian Markov Chain Monte Carlo (MCMC) estimation in the Stan programming language using packages *rstan* (Stan Development Team, 2019) and *brms* (Bürkner, 2017, 2018). Data exploration was conducted following Zuur et al. 2010, with the package *lattice* (Sarkar, 2008). For each model, we ran four chains with 10,000 iterations each, and saved every 10th iteration after the first 1,500. We used diffuse priors, with a normal distribution for the intercept and betas, and a half-Cauchy distribution for the random effects (Zuur, Hilbe, & Ieno, 2015). We assessed mixing, checked for autocorrelation within the chains, and conducted graphical posterior predictive checks with the package *bayesplot* (Gabry & Mahr, 2019). We plotted the residuals against the fitted values and model covariates to assess model fit. For model selection, we used the package *loo* (Vehtari, Gabry, Yao, & Gelman, 2019) to calculate the approximate leave-one-out-cross-validation information criterion (LOOIC) and plotted each model's difference in expected log predictive density (elpd) compared with the best-fit model. We chose the simplest models when there were multiple models with standard errors of elpd that overlapped with zero. To assess the difference between factor levels for the terms in these simplest models, we used the package *emmeans* (Lenth, 2019) to conduct pairwise contrasts between the posterior distribution of the estimated marginal means for each factor level. We concluded that there was little evidence to support differences between those groups when the standard error of these contrasts overlapped with zero.

We quantified the effect of vegetation management on ant species composition using a multivariate generalized linear model in package *mvabund* (Wang, Naumann, Eddelbuettel, Wilshire, & Warton, 2019). Unlike distance-based analyses, this model-based approach can account for the confounding mean-variance relationships that exist with count data (Wang, Naumann, Wright, & Warton, 2012). We included the interaction between vegetation management and time, and the random effect block identity to account for spatial dependency. We assessed model fit by plotting Dunn-Smyths residuals against fitted values and model covariates. We used a negative binomial distribution. For model selection, we simplified the models in a stepwise manner using likelihood ratio tests and a Monte Carlo resampling scheme with 10,000 iterations and alpha of 0.05. We used the same test and resampling scheme on the final models to test the significance of model terms by conducting univariate (single species) models with adjusted *p*-values that corrected for multiple tests (Wang et al., 2012). To visualise the change in species composition, we used the package *boral* (Hui, 2018) to fit the final model as a latent variable model using MCMC estimation. We fitted posterior latent variable medians in ordination plots where the two axes represented the two most important axes of species variation.

Results

Ants were widespread, abundant, and speciose; we found 3507 ants across 68 species and all pitfall traps contained ants at the end of the sampling period. The most speciose genera were *Crematogaster* (seven species), *Hypoponera* (seven species), *Tetramorium* (six species), and *Cardiocondyla* (four species). Species abundance was highly uneven (Fig. 1). The most abundant species was *Pheidole* sp. (5) (these bracketed numbers are unique species identifiers, which are listed with species abundances in Appendix: Table 1), though this may have been a multispecies complex (1271 individuals in 60.7% of traps). The next most abundant were *Monomorium* sp. (58) (434 individuals in 42% of traps), *Odontoponera denticulata* (1) (286 individuals in 48% of traps), *Anoplolepis gracilipes* (2) (239 individuals in 33.3% of traps), *Carebara* sp. (38) (187 individuals in 11.3% of traps), *Proatta butteli* (17) (183 individuals in 19.3% of traps), and *Odontomachus* sp. (10) (137 individuals in 21.3% of traps). These seven species accounted for 78% of all ant individuals found and 50% of all trap-level species occurrences (i.e., when each species was recorded as being present or absent in each trap), and the four most abundant accounted for 64% of individuals found and 38% of trap species occurrences. There were fifteen singletons and seven doubletons. The species accumulation curve showed that sampling was nearing completion (Fig. S2).

Vegetation management affected ant abundance, but not species richness, species evenness, or beta diversity (see Table 1 for mean values). The final model for ant abundance included the interaction between vegetation management and time (Fig. S3 and Appendix Table 2). Pairwise contrasts showed that pre-treatment ant abundance was the same in all

treatments, but post-treatment abundance was higher in the normal and enhanced plots than in the reduced plots, indicating that removing understory vegetation negatively affected ant abundance (Fig. 2(A)). Model estimates of post-treatment abundance, taken from the median of the posterior predictions, showed that abundance in the normal and enhanced treatments was respectively 86% and 58% higher than in the reduced treatment (Fig. 2(A)). Vegetation management did not affect species richness or evenness and it was removed from the final models for both variables (see Fig. S3 for model selection and Appendix Table 2 for model output). Species richness and evenness increased through time (Fig. 2 (B) and (C)), with the models predicting an increase of 19% and 3% post-treatment, respectively.

The final model for ant community composition included vegetation management, but as it did not include an interaction with time (LR (likelihood ratio) = 82, $P=0.079$), the differences between the treatments (Fig. 3(B) and (G)) represented pre-existing variation between the plots, as opposed to differences caused by the treatments themselves. Time was an important determinant of species composition (LR=160, $P=0.001$), as shown by the limited overlap between the polygons in Fig. 3 (A). Univariate species comparisons indicated that *Tapinoma melanocephalum* (29) (Fig. 3(C), LR=17, $P=0.002$), *Monomorium* sp. (42) (Fig. 3(D), LR=10, $P=0.035$), *Monomorium* sp. (58) (Fig. 3(E), LR=28, $P=0.001$), and *Cardiocondyla* sp. (94) (Fig. 3(F), LR=10, $P=0.035$) significantly increased in abundance post-treatment (Fig. 3(C)–(F)).

Discussion

This study supports previous findings that ants are abundant in oil palm, and that their communities are dominated by a small number of species (Pfeiffer et al., 2008; Senior et al., 2013). In Malaysian rainforest the seven most common ground-foraging ants constituted 15% of ant occurrences, whereas in the neighbouring oil palm plantation they made up 35% (Fayle et al., 2010). In another Malaysian plantation they accounted for an even greater proportion, at 47% (Lucey & Hill, 2012). Here they accounted for a larger proportion still, at 50%. High unevenness, such as this, is associated with pest outbreaks in agriculture (Crowder et al., 2010). The effect of unevenness has not been directly tested in oil palm. However, in addition to low species richness (Fayle et al., 2011), it is likely to be an important contributor to the reduction in ant-mediated ecosystem functions, such as predation and resource removal, in oil palm compared with forest (Gray et al., 2015; Nurdiansyah et al., 2016). In addition to reducing the magnitude of functioning, ecosystems with lower species evenness are more vulnerable to the negative impacts of environmental stress on functioning (Wittebolle et al., 2009). With clear evidence that intensifying climate change is stressing ecosystems (Walther et al., 2002), the high unevenness observed here is cause for concern about the future stability of these important systems.

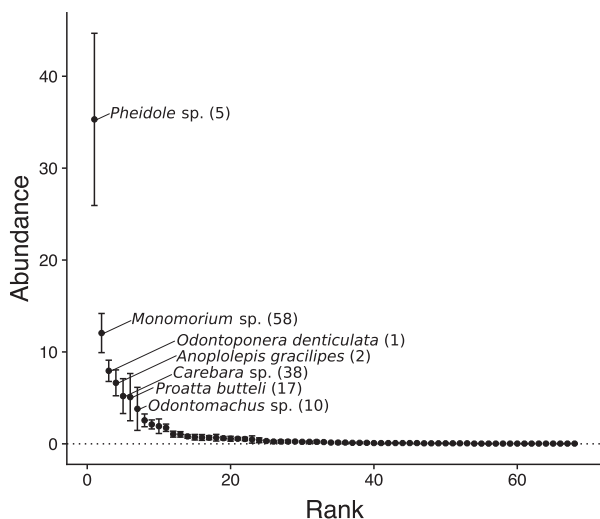


Fig. 1. A ranked species abundance plot with black dots showing the mean and error bars showing the standard error of species abundance by plot. Species names are given for the seven most abundant species. Bracketed numbers are unique species identifiers. The dotted line marks the zero level.

Table 1. A summary table showing the mean abundance, mean species richness, mean species evenness, and beta-diversity in the reduced (R), normal (N), and enhanced (E) plots pre- and post-treatment. Numbers following \pm are standard error of the mean.

	Pre-treatment			Post-treatment			
	R	N	E	R	N	E	E
Abundance	76 \pm 20	62 \pm 11	73 \pm 19	83 \pm 9	159 \pm 47	131 \pm 31	
Species richness	12 \pm 1.1	13 \pm 0.8	14 \pm 3.0	15 \pm 1.5	15 \pm 0.8	16 \pm 1.1	
Species evenness	0.73 \pm 0.03	0.71 \pm 0.08	0.80 \pm 0.02	0.83 \pm 0.01	0.64 \pm 0.09	0.84 \pm 0.03	
Beta diversity	0.64	0.71	0.53	0.61	0.66	0.57	

Future studies should investigate the ecological niches that the 61 rarer ant species found here occupy, as they represent an important component of ant biodiversity. They could be surviving in discrete sub-habitats in the oil palm plantation, such as in epiphytes, along streams, or in termite mounds, that require specific management practices to be maintained.

Removing the understory vegetation negatively impacted ant abundance, with \sim 58 to 86% more ants in the normal and enhanced plots compared with the reduced plots post-treatment. This reduction could potentially reduce ant-mediated ecosystem functions, such as pest-predation, resource removal, and bioturbation, the latter of which is crucial for maintaining soil health (Evans et al., 2011; Gray et al., 2015; Nurdiansyah et al., 2016; Tuma et al., 2019). In addition to the functions provided by ants directly, a reduction in ant abundance is also likely to indirectly affect other functions, such as decomposition and herbivory damage, through the release of ant prey populations (Parr et al., 2016). In other agricultural systems, the net effect of ants is typically beneficial for crop production; suppression experiments in tropical agriculture have shown that removing ants results in crop yield reductions of 30–50% (Evans et al., 2011; Gras et al., 2016; Wielgoss et al., 2014). Therefore, we advise that oil palm growers maintain a diverse understory to support this important taxon and that scientists investigate

further the impacts of reduced ant abundance under this management scenario. As there was no difference in ant abundance between the normal and enhanced plots, completely stopping applying herbicide is not necessary for supporting ground-foraging ants. However, as even limited chemical removal of vegetation such as that applied to the normal plots here can adversely affect other important taxa, such as Leopard Cats and belowground invertebrates (Ash-ton-Butt et al., 2018; Hood et al., 2019), we recommend that growers limit the use of herbicide wherever possible.

In contrast to the impact on ant abundance, removing understory vegetation did not affect ant species richness, species evenness, beta diversity, or community composition. This indicates that many of the species that are capable of surviving in oil palm plantations are open-habitat, disturbance-tolerant species that are fairly robust to altered understory management, and indeed two of the most abundant species that we found (*Odontoponera denticulata* and *Anoplolepis gracilipes*) commonly inhabit disturbed habitats (Pfeiffer et al., 2008; Yamane, 2009). Despite being robust to the removal of understory vegetation, which was dense and grew to several metres high in our plots (Luke, Advento, et al., 2019), species richness, species evenness, and community composition changed markedly through time. This indicates that there are factors unrelated to understory

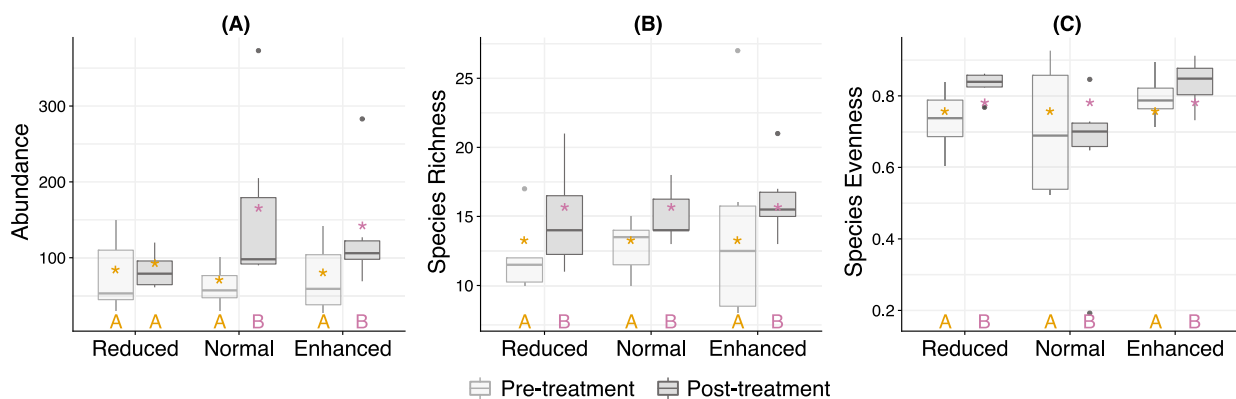


Fig. 2. Boxplots showing the median and interquartile ranges (IQR) of (A) ant abundance, (B) species richness, and (C) species evenness by vegetation management and time. Whiskers incorporate data that are $1.5 \times$ IQR and data beyond the whiskers are shown as individual points, with each point representing one plot. Asterisks show the expected median values for each group according to the simplest model of best-fit. Different letters and colours show differences between groups determined by (A) post-hoc comparisons (as all terms were included in the final model) or (B) and (C) the model simplification process (as vegetation management was removed from the final models).

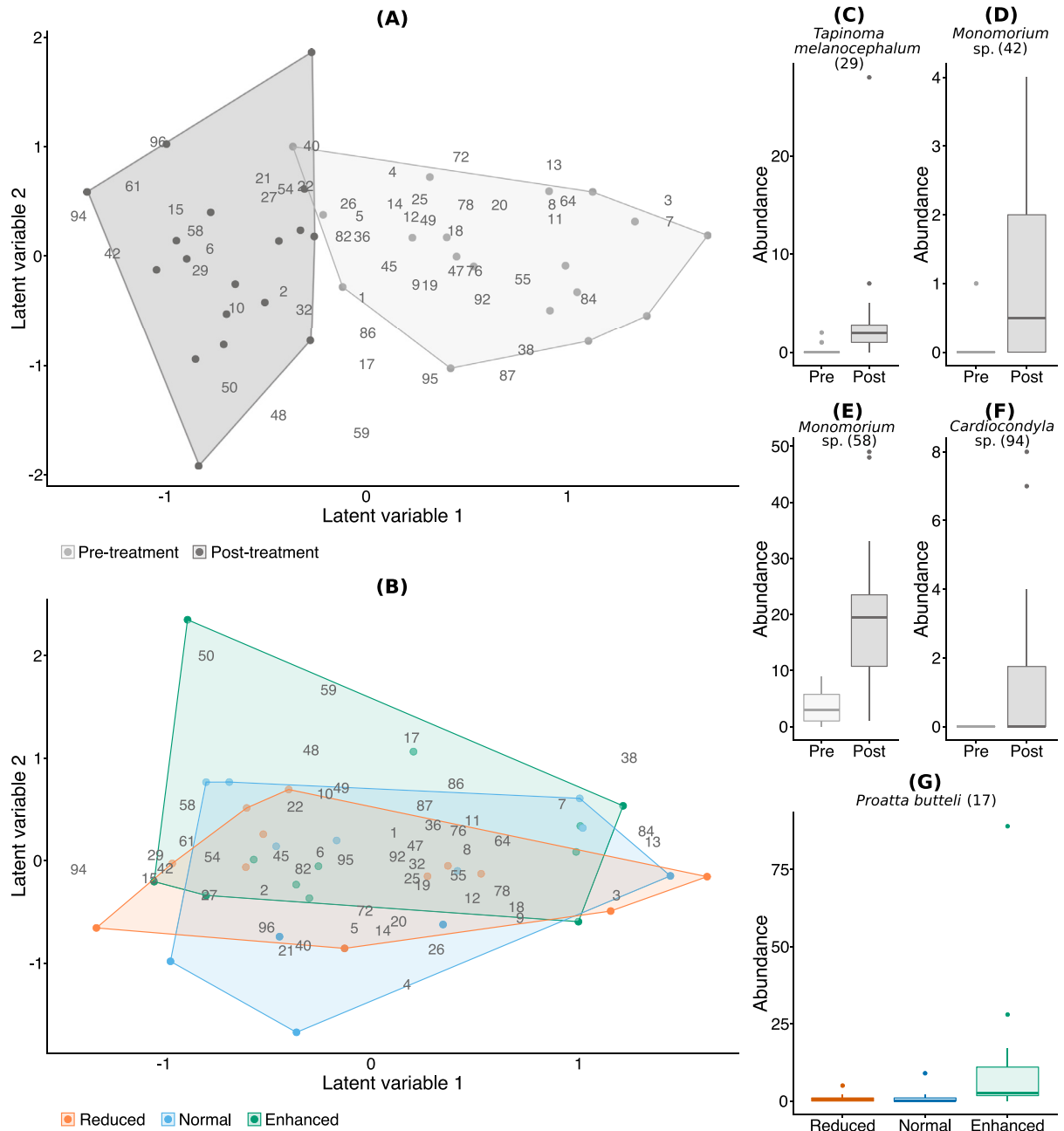


Fig. 3. (A) and (B) Latent variable model-based ordinations showing the multivariate and (C)–(G) boxplots showing the significant univariate changes in ant community composition according to the final model chosen. Plots are (A), (C)–(F) shaded by time or (B,G) coloured by vegetation management. (A) and (B) Each point is a single plot and minimum convex polygons overlaid. (C)–(G) Boxplots showing the abundance of: (C) *Tapinoma melanocephalum* (29), (D) *Monomorium* sp. (42), (E) *Monomorium* sp. (58), and (F) *Cardiocondyla* sp. (94) against time, and (G) *Proatta butтели* (17) against vegetation management. Bracketed (C–G) and plotted (A) and (B) numbers are unique identifiers for the ant species, given in Appendix: Table 1. Boxplots were calculated as in Fig. 2. The final model did not include the interaction between vegetation management and time. Therefore, although there are significant differences between the treatments in (B) and (G), these represent pre-existing variation between the plots as opposed to differences caused by the treatments themselves.

management that impact ground-foraging ant communities in oil palm. The compositional changes observed here could be caused by annual climatic fluctuations, as pre-treatment samples were taken during the dry season and post-treatment samples were taken during the wet season, or they could represent a longer-term shift. They are unlikely to represent

successional changes (Wang & Foster, 2016), as the plantations in this study were old, similar in age (20–26 years old), and the study period was relatively short (18 months). Ultimately, it is not possible to determine what caused this shift with our data. We suggest that future studies investigate which factors could cause this, particularly considering the

potential fragility of this system due to its highly uneven composition (Crowder et al., 2010; Wittebolle et al., 2009).

This study found that the common practice of removing understory vegetation in oil palm plantations through the liberal application of herbicides (Corley & Tinker, 2015; Wibawa et al., 2007) negatively impacts ground-foraging ants. It supports previous findings that greater habitat complexity in oil palm plantations promotes important biodiversity and enhances ecosystem functioning (Ashton-Butt et al., 2018; Darras et al., 2019; Hood et al., 2019; Nájera & Simonetti, 2010). Therefore, we advise that oil palm growers limit the application of herbicides to benefit biodiversity and production. This evidence-based guidance should be used to inform policy and certification schemes, such as Principle 7 of the Roundtable on Sustainable Palm Oil's Principles and Criteria for the Production of Sustainable Palm Oil, which calls for reduced pesticide application, adoption of integrated pest management (IPM) techniques, and preservation of biodiversity where possible (Roundtable on Sustainable Palm Oil (RSPO), 2018). Future studies should investigate the impact of understory vegetation management in younger plantations, as they do not have the microclimatic buffer of a closed canopy (Luskin & Potts, 2011). The removal of vegetation in these habitats could result in more drastic changes in ground temperature and aridity. Furthermore, species composition, including ground-foraging ants (Wang & Foster, 2016), differs from that in mature plantations, and the species in younger plantations may be more vulnerable to disturbance. With vast swathes of land now due to be replanted (Snaddon, Willis, & Macdonald, 2013), this is an urgent research priority (Padfield et al., 2019).

Declaration of Competing Interest

Co-authors listed with a Sinar Mas Agro Resources and Technology Research Institute (SMARTRI) affiliation were employed by SMARTRI, which is the research division of Golden Agri Resources (GAR), at the time of the study. The BEFTA Programme is co-funded by GAR. There is an MOU in place that protects the data-use and intellectual freedom of all researchers on the project. Therefore, the programme represents a collaboration between the University of Cambridge and an oil palm company that maintains academic independence whilst ensuring that the results are readily disseminated to inform best management practices.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2020.07.002](https://doi.org/10.1016/j.baae.2020.07.002).

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