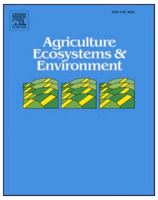
Agriculture, Ecosystems and Environment 373 (2024) 109102

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee



Conversion of rainforest to both traditional and industrial oil palm systems changes the biodiversity, web-building, and prey capture of understory spiders (Liberia, West Africa)

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ARTICLE INFO

Keywords:
Land use change
Araneae
Tropical agriculture
Elaeis guineensis

ABSTRACT

Oil palm (*Elaeis guineensis*) is a tropical crop that produces palm oil: the most traded vegetable oil worldwide. It is principally grown in Southeast Asia, but West Africa – oil palm's native range – is rapidly becoming a hotspot of cultivation. Oil palm in West Africa is cultivated using both traditional (i.e., by local people) and industrial (i.e., by corporations) approaches. Little is known about the relative ecological impacts of these different oil palm cultivation styles on native rainforest ecosystems. Working in Liberia within the framework of the Sustainable Oil Palm in West Africa (SOPWA) Project, we investigated the impacts of traditional and industrial approaches to oil palm cultivation on spiders—important meso-predators that provide pest control services—inhabiting understory vegetation. We sampled spiders in three systems: (1) rainforest, (2) fallowed farmland with wild-growing oil palms, which local people manage and harvest ('country palm'), and (3) industrial oil palm farms. We assessed differences in the abundance of all spiders, adults only, and juveniles only; spider species richness, and spider species-level community composition. Through focussed samples of orb web-building spiders, we also assessed differences in spider web-building (the average web area, total web area, standard deviation of web area) and prey capture (the average captured prey, total captured prey, standard deviation of captured prey) across systems. We found that rainforest had more species in total and on average than country palm and industrial oil palm, and that country palm had fewer spider individuals than rainforest and industrial oil palm. All systems supported distinct spider communities. Our focussed studies on orb web-building spiders indicated that the average web area, total web area, and standard deviation of web area were all higher in industrial oil palm than forest and country palm, which led to higher average and total prey capture. Our findings indicate that conversion of rainforest to country palm and industrial oil palm in Liberia has negative effects on spider biodiversity, with clear "winning" and "losing" species, and levels of spider-associated ecosystem functioning. Our findings also show that industrial oil palm farms can support relatively abundant and speciose spider communities, which may provide important pest control services that could boost oil palm productivity. Future work is needed to identify effective management strategies to conserve spiders and associated pest control services in West African country palm and industrial oil palm systems.

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https://doi.org/10.1016/j.agee.2024.109102
Received 15 December 2023; Received in revised form 7 May 2024; Accepted 29 May 2024

1. Introduction

Agricultural production has transformed landscapes worldwide (Ramankutty et al., 2018). While cultivation is needed for food security, and provides jobs and income to millions of people, conversion of native habitat to farmlands and pasture has also caused widespread biodiversity loss and changes in ecosystem functioning (Foley et al., 2005; Ramankutty et al., 2018). Although agricultural expansion has slowed globally in recent years, this trend has been driven largely by reduced agricultural activity in temperate regions (Ramankutty et al., 2018). In comparison, in the tropics, vast areas of land are still being converted to agriculture, threatening the high number of species found in tropical landscapes (Pendrill et al., 2022; Ramankutty et al., 2018).

Oil palm (*Elaeis guineensis*) is a vegetable oil-producing crop that is grown across the tropics to produce palm oil and palm kernel oil (hereafter, collectively called palm oil) (Meijaard et al., 2020). Palm oil is the most widely produced and traded vegetable oil worldwide (about 76 million metric tons produced in 2021/2022 fiscal year; (USDA, 2023)), and oil palm agriculture now covers over 21 million hectares of land globally (Descals et al., 2021). Oil palm expansion has frequently occurred at the expense of natural habitat, with large areas of rainforest (and, to a lesser extent, savannah and peatland) being turned into oil palm plantations (Meijaard et al., 2020). Converting rainforest to oil palm plantations reduces the diversity and structural complexity of understory and overstory vegetation (Foster et al., 2011; Luskin and Potts, 2011; Rembold et al., 2017), resulting in hotter, drier, and more variable microclimates (Luskin and Potts, 2011; Meijide et al., 2018; Williamson et al., 2021), lower levels of biodiversity (Drescher et al., 2016; Foster et al., 2011), and changes in rates of ecosystem functions, such as decomposition and predation (Barnes et al., 2017, 2014; Dislich et al., 2017). These changes caused by oil palm cultivation are concerning from both conservation and crop management perspectives, since many species contribute valuable ecosystem services (e.g., pest control) that can improve oil palm health and yield (Dislich et al., 2017; Luke et al., 2020).

Oil palm is principally grown in Southeast Asia, but production is also increasing rapidly in other parts of the tropics, including West and Central Africa (Davis et al., 2020; Pashkevich et al., 2024). Oil palm is native to West and Central Africa, and local people have harvested wild-growing oil palms in the region for at least 3000 years (Kay et al., 2019). Here, oil palm is grown using industrial (i.e., large-scale cultivation managed by corporations), smallholder (small- to medium-scale cultivation managed by individual farmers), and traditional management approaches (harvesting from wild-growing oil palms that grow naturally in low-lying areas of rainforest). West African oil palm production is expanding rapidly in many areas, owing to a perceived ample land availability, suitable climate for oil palm growth (although this is disputed owing to lower levels of solar radiation in comparison to Southeast Asia (Woittiez et al., 2017)), cheap labour costs, and rapid urbanization that has increased demand for market-purchasable palm oil rather than harvesting of wild-growing palm fruits (Meijaard et al., 2018; Ordway et al., 2017). In comparison to Southeast Asia, very little is known about how oil palm cultivation in West Africa affects nature and society, or whether this differs between industrial, smallholder, or traditionally-managed farms (Pashkevich et al., 2024; Reiss-Woolever et al., 2022). Patterns observed in Southeast Asia are unlikely to play out consistently in West Africa, owing to locally unique ecological and socioeconomic contexts. Expansion of the West African palm oil industry could improve local livelihoods and food security in the region, but unsustainable expansion that does not consider local ecosystems and traditional ways of life could cause substantial negative impacts to nature and society.

Spiders (Arthropoda: Arachnida, Araneae) are important mesopredators that are abundant in nearly all terrestrial systems (Piel, 2018). In tropical croplands, such as oil palm plantations, spiders are a key component of invertebrate food webs (serving as both prey and predator) and contribute to pest management by predating insects that damage crops (Michalko et al., 2019; Pashkevich et al., 2022). In a meta-analysis, Michalko et al. (2019) found that spiders reduced the abundance of agricultural pests in 79 % of cases. Previous studies in Southeast Asia have shown that oil palm cultivation negatively affects spiders in native rainforest. For instance, working in the ground and leaf litter microhabitats, Potapov et al. (2020) found that converting rainforest to smallholder oil palm plantations reduced the density and species richness of spiders by 54–90 % and 57–98 % on average, respectively, and changed spider species-level community composition. Working in the same sites but studying jumping spiders (family Salticidae) in the canopy, Junggebauer et al. (2021) found that oil palm plantations had 70 % fewer species on average than rainforest, and supported different spider communities, but that spider abundance did not differ between systems. These changes are likely driven by differences in habitat complexity, microclimate, and prey availability between rainforest and oil palm systems. In comparison to rainforest, oil palm plantations have less diverse and structurally complex plant communities (Rembold et al., 2017), which spiders use for hunting and reproduction, and are drier, hotter and have more variable temperatures across the day (Luskin and Potts, 2011; Meijide et al., 2018; Pashkevich et al., 2024), potentially increasing the risk of spider desiccation and affecting the availability of insect prey (Barnes et al., 2014; Mumme et al., 2015). Despite these between-systems differences, oil palm plantations can still support relatively abundant and speciose spider communities. For instance, working in industrial oil palm plantations in Indonesia, Pashkevich et al. (2021) found 131 spider morphospecies across the canopy, understory, and ground microhabitats (although male and female specimens were not matched, and so real species counts would likely be lower). Spider biodiversity is generally severely unstudied across West Africa, especially in a systematic sampling context (Pekár et al., 2021), and very little work has assessed how agricultural cultivation in the region affects spiders. Addressing these knowledge gaps is important for both establishing baseline biodiversity data in West Africa to inform future conservation efforts, and for increasing the productivity of West African oil palm systems through the pest control services that spiders provide.

In this study, we investigated how traditional and industrial approaches to oil palm cultivation in Liberia, West Africa affect the biodiversity, web-building, and prey capture of spiders in understory vegetation. Working in the framework of the Sustainable Oil Palm in West Africa (SOPWA) Project (Pashkevich et al., 2024), we quantified spider communities in the understory across a network of plots in rainforest (native habitat); fallowed farmland with wild-growing oil palms, which local people manage and harvest (called ‘country palm’ by local people); and industrial oil palm farms (we use “farm” rather than “plantation”, as is common in Southeast Asia, in line with the local West African vernacular). We aimed to assess how traditional and industrial oil palm cultivation affects: (1) the abundance of all spiders, adults only, and juveniles only; spider species richness; and spider species-level community composition; (2) the average, total, and the standard deviation of web area of orb web-building spiders (families Araneidae, Tetragnathidae, Theridiosomatidae, and Uloboridae); (3) the average, total, and the standard deviation of prey captured, and the proportion of webs with captured prey, of orb web-building spiders.

2. Methods

2.1. Site

Fieldwork occurred in Sinoe County, Liberia as part of the Sustainable Oil Palm in West Africa (SOPWA) Project (5.135195 N, 9.078423 W; Fig. 1). The SOPWA Project is a large-scale, well-replicated, field-based study that is investigating how traditional and industrial approaches to oil palm cultivation affect rainforest ecosystems (Pashkevich et al., 2024). The typical flora of Sinoe County is lowland evergreen rainforest, and Sinoe County is a globally recognised biodiversity hotspot (Myers et al., 2000; Olson et al., 2001). Liberia as a whole retains the highest density of rainforest in West Africa, although about one-fifth of its forested area has been lost to agriculture, logging, and mining activities (Davis et al., 2020). Land development has increased rapidly since 2003, when 15 years of domestic conflict ended (First Liberian Civil War: 1989–1997; Second Liberian Civil War: 1999–2003), and after which the Government of Liberia allowed foreign investors to acquire large areas of land as part of its economic re-development plan (Davis et al., 2020).

Traditionally, local people in Sinoe County have relied on shifting cultivation for their livelihoods, burning small areas of rainforest annually (typically around 1 ha) to grow crops (mainly rice, cassava, cucumber, pepper, and bitterball) for consumption (Pashkevich et al., 2024). When preparing lands for farming, local people often choose areas with wild-growing oil palms (called ‘country palms’ by local communities), which survive the burning process or grow-up after the area is left fallow (typically after one or two years). The density of palms varies, but care is taken so that crops such as cassava still receive sunlight, even after the country palms are fully grown. Country palms are a food staple in this region, with local people harvesting the palm fruits to produce palm oil, eat fresh, or to produce palm wine (Marshall and Hawthorne, 2012).

Oil palm is also cultivated in Sinoe County in industrial farms, most of which were established by Golden Veroleum Liberia (GVL). GVL is the largest oil palm developer in Liberia and a member of the Golden Agri-Resources (GAR) group, based in Singapore, that manages oil palm farms in thirteen countries. GVL has a concession area, leased from the Government of Liberia, of 220,000 ha of non-private land across the Counties of Sinoe, Grand Kru, Maryland, River Cess, and River Gee. GVL is currently cultivating oil palm on ~ 19000 ha, and has set-aside almost 11500 ha as High Conservation Value (HCV) areas (i.e., forested areas with recognised value to ecosystems or society) (Wright and Tumbey Jr, 2012). GVL established its first oil palm farms in Sinoe County in 2012, and currently has six oil palm farms in the County: Tarjuowon-North, Tarjuowon-South, Butaw, Kpayan, Tartweh, and Kabada.

To assess the effects of oil palm cultivation on spiders, we sampled spiders within the SOPWA Project’s ecological monitoring plots (measuring 50 ×50 m), which are located in three distinct systems (Pashkevich et al., 2024):

1) *Forest* – These plots are in areas of old-growth Upper Guinean lowland rainforest, with no record of large-scale disturbance. These areas are owned by GVL, but used by local people for hunting, harvesting of non-timber forest products (NTFPs), and spiritual and cultural purposes. Rainforest is an ideal reference habitat, as nearly 90 % of Sinoe County is forested, and forest is frequently converted to new farms in the region (Pashkevich et al., 2024).

2) *Country palm* – These plots are in fallowed traditional smallholder farms, which we identified by asking local community members where they harvested their oil palm fruits. Areas have not been farmed for at least two years (mean: 7.6 years; range: 2 – 30 years; (Pashkevich et al., 2024), and therefore represent areas of dense, young regrowth (called “low bush” by local communities). Local people return to these areas to harvest wild-growing oil palms (called “country palms” locally). These palms either survived the burning process used to establish the smallholder farms, or grew-up naturally after farming activities stopped. At the time of farming, various planted crops were harvested alongside the country palms (typically cassava but also rice, pumpkin, cucumber,

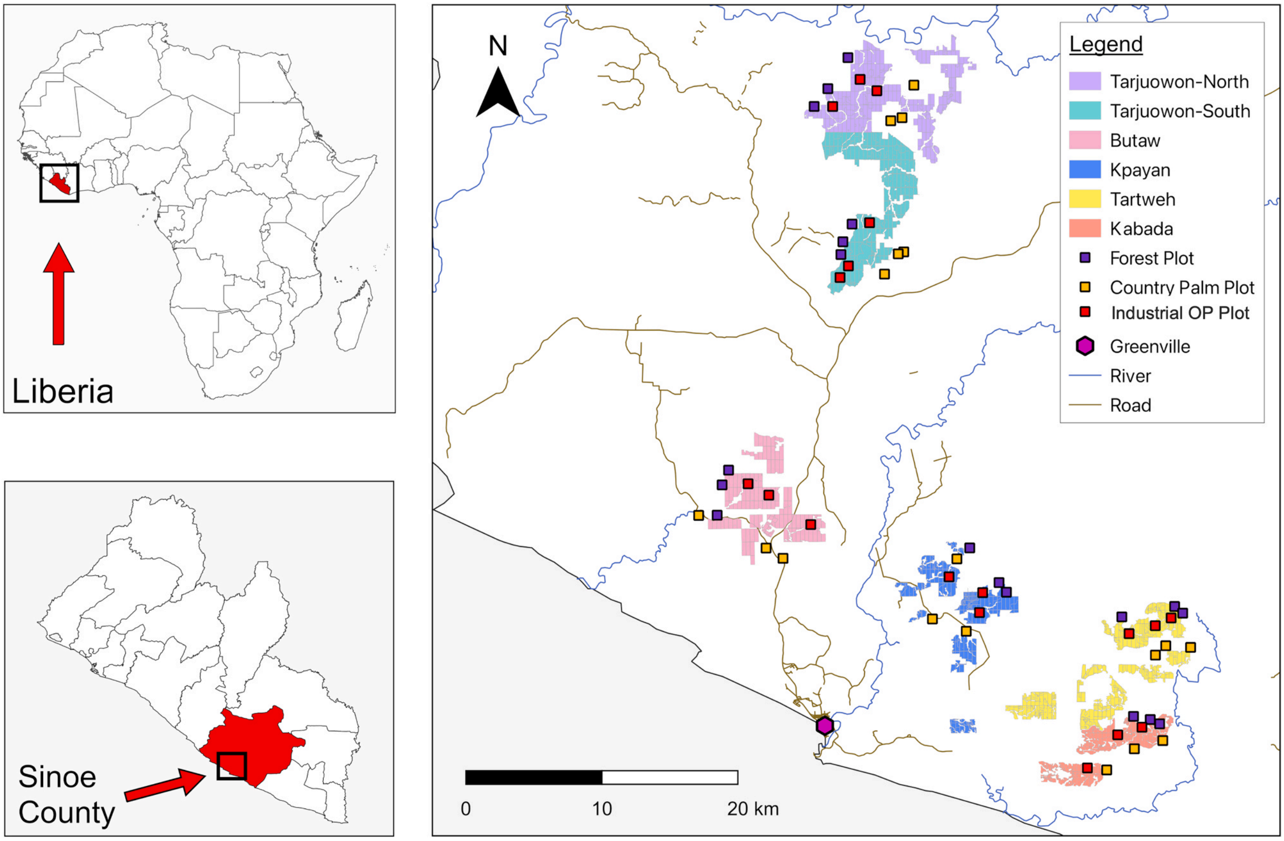

Fig. 1. Map of the SOPWA Project study area in Sinoe County, Liberia. The SOPWA Project features study plots (50 ×50 m) in forest (N = 18; purple squares), country palm (N = 18; orange squares), and industrial oil palm (‘Industrial OP’ in legend, N = 18; red squares) systems. Plots are spatially clustered in and around each of six industrial oil palm farms: Tarjuowon-North (purple), Tarjuowon-South (turquoise), Butaw (pink), Kpayan (blue), Tartweh (yellow), and Kabada (peach). The city of Greenville (pink hexagon), the capital of Sinoe County, is shown as a reference. Blue and brown lines indicate major rivers and roads, respectively. For a full description of the SOPWA Project, see Pashkevich et al. (2024).

pepper, and bitterball; (Pashkevich et al., 2024). These crops are grown in the understory on a long rotation cycle to maintain soil fertility. Chemical fertilisers, herbicides, or pesticides have never been applied within these plots.

3) *Industrial oil palm* – These plots are in GVL oil palm farms. Farms are oil palm monocultures and organised into 300 ×1000 m blocks, separated by dirt roads, with palms planted approximately 8 m apart in a staggered design. The farms within which we work are not managed identically, but all are managed according to business-as-usual practices that were developed in Sumatra, Indonesia, including regular application of fertilisers, herbicides, and pesticides (when outbreaks of insect pests occur). Planted palms are of high-yielding varieties and are harvested manually (using a chisel or sickle on a telescopic pole, depending on palm age) at 10–15 day intervals. At the time of sampling, palms in these plots were between four and ten years old (i.e., all were fruiting), with 50 % of plots having palms aged six or seven years (Pashkevich et al., 2024).

Plots are arranged in six clusters, located in and around each of the six GVL oil palm farms in Sinoe County (Fig. 1). There are nine plots in each cluster (three plots per system per cluster; 54 plots total), ensuring that same-system plots within a cluster are at least 400 m apart. See Pashkevich et al. (2024) for full details of the SOPWA Project study design. Before any fieldwork, we held meetings with local communities, chaired by local leaders, and obtained prior informed consent for our work. Ethical approval for interactions with local communities was obtained from the Cambridge Psychology Research Ethics Committee (Application number: PRE.2020.004). During these meetings, we recruited two people from the community to work with us as local guides, paying a standard accepted daily rate.

2.2. Data collection

Data collection occurred from February – March 2022, during the regional dry season. We sampled spiders living in the understory vegetation from all study plots (N = 54). When sampling, we semi-randomly alternated the order in which we visited systems each day to mitigate potential confounding impacts of survey time on our findings. We collected spiders by walking a 100 m transect in each plot, representing two randomly chosen and adjacent sides of the plot, and collecting all spiders found above the ground and within 1 m of the observer's reach. A single observer (MDP) collected all spiders to ensure consistent detection of spiders across samples (Coddington et al., 1996). A headtorch was always used while sampling to mitigate the potential for cross-system differences in canopy openness and light levels (Pashkevich et al., 2024) influencing detection of spiders. Owing to plot corners, our transects each represented a total survey area of 204 m^2. Prior to collecting orb web-building spiders (families Araneidae, Tetragnathidae, Theridiosomatidae, and Uloboridae), we additionally recorded the length and width of each of their webs to the nearest centimetre, and the number of insect prey present in each web. We recorded web and prey data for orb web-building spiders only, as this web shape and the insect prey within were easily measurable, and orb web-building spider families were found commonly in all plots. We only collected during the day (09:00 – 17:00) and when conditions were dry. We sampled spiders from all plots in a cluster before moving onto the next cluster (Fig. 1). We exported the spiders to University of Cambridge (permit number MD/048/2022/-1). Spiders were identified using stereoscopes typically (AmScope ZM- 4 T), with occasional use of compound scopes (Olympus BX61) for genitalia examination. Adults and juveniles were separated, and juveniles were identified to family where possible. Keys to spider families were utilised (e.g. Jocqué and Dippenaar-Schoeman, 2006) alongside more up-to-date information on the majority of spider families from the World Spider Catalog (2023). We identified adults to morphospecies level (hereafter, 'species'), matching males and females of the same species. The spiders are preserved currently in 70 % ethanol at the University Museum of Zoology Cambridge (Cambridge, UK), and we are progressing conversations with the Government of Liberia to repatriate a full voucher series to support future spider work in the region.

2.3. Statistical analyses

We conducted all statistical analyses in *R* (version 4.2.0; (R Core Team, 2022)) using *RStudio* (version 2022.02.3+492; (RStudio Team, 2022)). We used *tidyverse* (Wickham et al., 2019) for data exploration, wrangling, and visualisation; *iNEXT* (Hsieh et al., 2016) for species accumulation curves; *vegan* (Oksanen et al., 2022) and *BiodiversityR* (Kindt, 2022) for rank abundance curves; *glmmTMB* (Magnusson et al., 2019), *mvabund* (Wang et al., 2012), and *boral* (Hui, 2016) for fitting generalised linear mixed effects models (GLMMs), multivariate generalised linear models (mGLMs), and generalised linear latent variable models (GLLVMs) respectively; *DHARMa* for model validation (Hartig and Lohse, 2022); and *multcomp* (Hothorn et al., 2022) for post-hoc tests.

Unless otherwise stated, we fitted models to negative binomial distributions (log links), as we were analysing count data and poisson-distributed models were overdispersed. Our models included *System* (levels: forest, country palm, industrial oil palm) as a fixed effect, and *Farm* (levels: Tarjuowon-North, Tarjuowon-South, Butaw, Kpayan, Tartweh, Kabada) as a random intercept effect, to account for the spatial clustering of our plots and timing of sampling in our modelling ($Response \sim System + (1 \mid Farm)$). We validated our models by plotting Pearson residuals against fitted values and covariate *System* and verifying no patterns were present. We also simulated 10,000 datasets from our model, calculated the dispersion statistic for each simulated dataset, and verified that these values tracked the dispersion statistic of our model (Zuur and Ieno, 2016). Our simulations indicated no issues with our modelling. We determined if *System* affected each response ($P < 0.05$) by comparing our GLMMs to null models ($Response \sim 1 + (1 \mid Farm)$) using likelihood ratio tests (LRTs). If *System* only moderately affected the response ($0.01 < P < 0.07$), we re-calculated *P*-values based on parametric bootstrapping, as a sensitivity analysis. When *System* was significant ($P < 0.05$), we conducted pairwise post-hoc tests (using Tukey all-pair comparison tests) to determine differences between systems, accounting for multiple comparisons. We only report significant pairwise comparisons; all unreported pairwise comparisons indicate systems that were not significantly different.

2.3.1. Impacts of traditional and industrial approaches to oil palm cultivation on spider abundance, richness, and community composition

To assess our sampling completeness, we calculated and plotted interpolated and extrapolated species accumulation curves for each system, extrapolating to double the number of observed individuals. We assessed species evenness within each system by plotting rank abundance curves. We included only adult spiders in these analyses.

We used GLMMs to assess differences in the abundance of all spiders, adults-only, and juveniles-only, and spider species richness in the understory across rainforest, country palm, and industrial oil palm systems. We separately assessed differences in the abundance of all spiders, adults-only, and juveniles-only, to determine whether rainforest conversion affected spiders differently across their life cycle. We used a mGLM to assess differences in the species-level composition of spiders in the understory across systems (Wang et al., 2012). We fitted our mGLM to a poisson distribution, as model validation did not indicate that a negative binomial distribution was needed. We validated our mGLM by plotting Dunn-Smyth residuals against fitted values and covariate *System* and verifying no patterns were present. We determined if *System* affected the species-level composition of understory spiders using a LRT and by bootstrapping probability integral transform (PIT) residuals, using 10, 000 resampling iterations (Warton et al., 2017). When doing so, we included *Farm* as a blocking variable, to account for the spatial arrangement of plots and timing of sampling in our modelling. As *System* was significant ($P < 0.05$), we ran univariate analyses to identify specific spider species with significant changes in abundance across systems.

Univariate P-values were corrected for multiple testing using a step-down resampling algorithm (Wang et al., 2012). We additionally visualised our species-level composition findings by plotting the posterior medians of a Bayesian GLLVM as an ordination (Hui, 2016). This statistical technique is a model-based equivalent to traditional distance-based approaches, such as non-metric multidimensional scaling (NMDS) (Hui, 2016). To do this, we fitted a pure (i.e., no covariates included) GLLVM using a poisson distribution, including *Farm* as a random row effect, to account for the spatial arrangement of plots and timing of sampling in our modelling, and two latent variables (LVs). We fitted normal priors (mean zero, variance 10) on column-specific intercepts, normal priors (mean zero, variance 10) on column-specific intercepts and latent variable coefficients, and half-Cauchy priors (mean zero, variance 5) on the standard deviation of the random effects normal distribution. We ran models for 50,000 iterations (one chain, thinning rate of 10), discarding the first 8000 iterations as burn-in. We validated GLLVMs by inspecting MCMC trace plots, and ensuring that no patterns were present when Dunn-Smyth residuals were plotted against linear predictors, row indices, and column indices (Hui, 2016). To aid visualisation of our ordination, we drew polygons around points belonging to the same *System*. We concluded that meaningful differences existed when polygons had lower levels of overlap.

2.3.2. *Impacts of traditional and industrial approaches to oil palm cultivation on spider web-building*

We used GLMMs to assess differences in the average web area (i.e., the mean area of webs along a transect), total web area (i.e., the summed area of webs along a transect), and standard deviation of web area (i.e., the variation in area of webs along a transect) across rainforest, country palm, and industrial oil palm systems. We calculated average web area and total web area by multiplying the length and width of each web along a transect, and taking the mean and sum, respectively. We calculated the standard deviation of web area by taking the square-root of the variance in web area along a transect. We removed one ‘Country palm’ sample prior to this analysis, as no web-building spiders were found and therefore the standard deviation of web area could not be calculated ($N = 53$). We rounded the average web area and standard deviation of web area per plot to the nearest integer to meet model assumptions.

2.3.3. *Impacts of traditional and industrial approaches to oil palm cultivation on spider prey capture*

We used GLMMs to assess differences in the average captured prey (i.e., the mean number of captured prey per web along a transect), total captured prey (i.e., the summed number of captured prey across all webs along a transect), standard deviation of captured prey (i.e., the variation in number of captured prey across webs along a transect), and proportion of webs with captured prey (i.e., the percent of webs along a transect having captured prey) across rainforest, country palm, and industrial oil palm systems. As a sensitivity analysis, we also assessed differences in number of prey captured per web area, to test whether any significant variation in captured prey was related to differences in total webbing across systems. Prior to analysis, we removed one country palm sample, as described above, as no web-building spiders (and therefore no prey) were present ($N = 53$). We calculated average captured prey and total captured prey by taking the mean and total number of insect prey in webs along each transect. We calculated the standard deviation of captured prey by taking the square-root of the variance in captured prey within webs along a transect. Prior to analysis, we multiplied the average captured prey and standard deviation of captured prey by 100, and rounded to the nearest integer, to meet model assumptions. These values therefore reflect captured prey per 100 webs. As the proportion of webs with captured prey was a continuous variable bounded between 0 and 1 inclusive, we analysed these data using a model fitted to a beta distribution. Prior to analysis, we transformed our data to be between 0 and 1 using the equation:

$$(Y * (N - 1) + 0.5) / N$$

Wherein Y = the proportion of webs along a transect with insect prey, and N = the total number of webs across all samples (Cribari-Neto and Zeileis, 2010). Prior to our sensitivity analysis, and to meet model assumptions, we calculated captured prey per web area using the equation:

$$((P / W) * 1 \times 10^{6}) / 204$$

Wherein P = the total captured prey along a transect, and W = the total web area along a transect. Our equation scales-up the area surveyed during our transects (204 m^2) to an area of 100 ha (1×10^6 m^2), to facilitate intuitive interpretation of the results and comparison with other studies (e.g., Spear, 2016).

3. Results

3.1. *Impacts of traditional and industrial approaches to oil palm cultivation on spider abundance, richness, and community composition*

We collected 2408 spiders and 100 spider species in total, including 864 spiders (278 adults and 59 species; 586 juveniles) in forest, 583 spiders (148 adults and 48 species; 435 juveniles) in country palm, and 961 spiders (266 adults and 36 species; 695 juveniles) in industrial oil palm. There was some, but not complete, overlap in species across systems (Fig. 2A). We were able to identify 2064 of the 2408 spiders to family. Six families (Araneidae, n = 602 spiders; Tetragnathidae, n = 484 spiders; Theridiidae, n = 270 spiders; Pholcidae, n = 197 spiders; Theridiosomatidae, n = 127 spiders; and Uloboridae, n = 125 spiders) accounted for 87 % (N = 1805 spiders) of all specimens. Species accumulation curves in all systems were starting to level-off, indicating our sampling effort captured most spider species (Fig. 2B). However, the species accumulation curve in country palm was still increasing, indicating that our sampling completeness in country palm was less than that in forest and industrial oil palm. Five species from three families accounted for 49 % of spiders in forest (Pholcidae sp. 2, n = 44; Pholcidae sp. 3, n = 40; Argyrodes sp. 2, n = 25; Theridiidae sp. 12, n = 15; Mysmenidae sp. 1, n = 13). Four species from three families accounted for 42 % of spiders in country palm (Mysmenidae sp. 1, n = 33; Pholcidae sp. 2, n = 9; Theridiosomatidae sp. 1, n = 9; Theridiosomatidae sp. 2, n = 8). Six species from four families accounted for 79 % of spiders in industrial oil palm (*Gasteracantha curvispina*, n = 78; Tetragnathidae sp. 1, n = 55; Araneidae sp. 3, n = 35; Theridiosomatidae sp. 1, n = 18; Tetragnathidae sp. 2, n = 12; Theridiidae sp. 25, n = 12) (Fig. 2C).

We found differences in the abundance of all spiders ($LRT_{System} = 18.085$, $P_{System} < 0.001$), adults only ($LRT_{System} = 15.775$, $P_{System} < 0.001$), and juveniles only ($LRT_{System} = 13.480$, $P_{System} = 0.001$) in the understory across forest, country palm, and industrial oil palm systems (Fig. 3A-C). Post-hoc analyses showed that the average abundance of all spiders, adults only, and juveniles only in forest (*All spiders:* $\overline{X}$ (mean) ± SE (standard error) = 48.0 ± 3.3; *Adults only:* 15.4 ± 1.4; *Juveniles only*: 32.6 ± 2.5) and industrial oil palm (*All spiders:* 53.4 ± 5.0; *Adults only:* 14.8 ± 2.1; *Juveniles only*: 38.6 ± 4.0) was 1.3–1.9 and 1.6–1.8 times greater than in country palm (*All spiders:* 32.4 ± 2.4; *Adults only:* 8.2 ± 0.9; *Juveniles only*: 24.2 ± 2.0), respectively ($P_{Comparisons} < 0.05$). We also found differences in the species richness of spiders in the understory across systems ($LRT_{System} = 15.850$, $P_{System} < 0.001$) (Fig. 3D). Post-hoc analyses showed that the average species richness of spiders in forest (8.5 ± 0.7) was 1.6 and 1.5 times greater than in country palm (5.3 ± 0.4) and industrial oil palm (5.7 ± 0.5), respectively ($P_{Comparisons} < 0.006$). We also found differences in the species-level community composition of spiders in the understory across studied systems ($LRT_{System} = 974.1$, $P_{System} < 0.001$) (Fig. 3E-F). Post-hoc analyses showed differences in species-level community composition between forest, country palm, and industrial oil palm systems ($P_{Comparisons} < 0.001$). Univariate analyses indicated that compositional differences

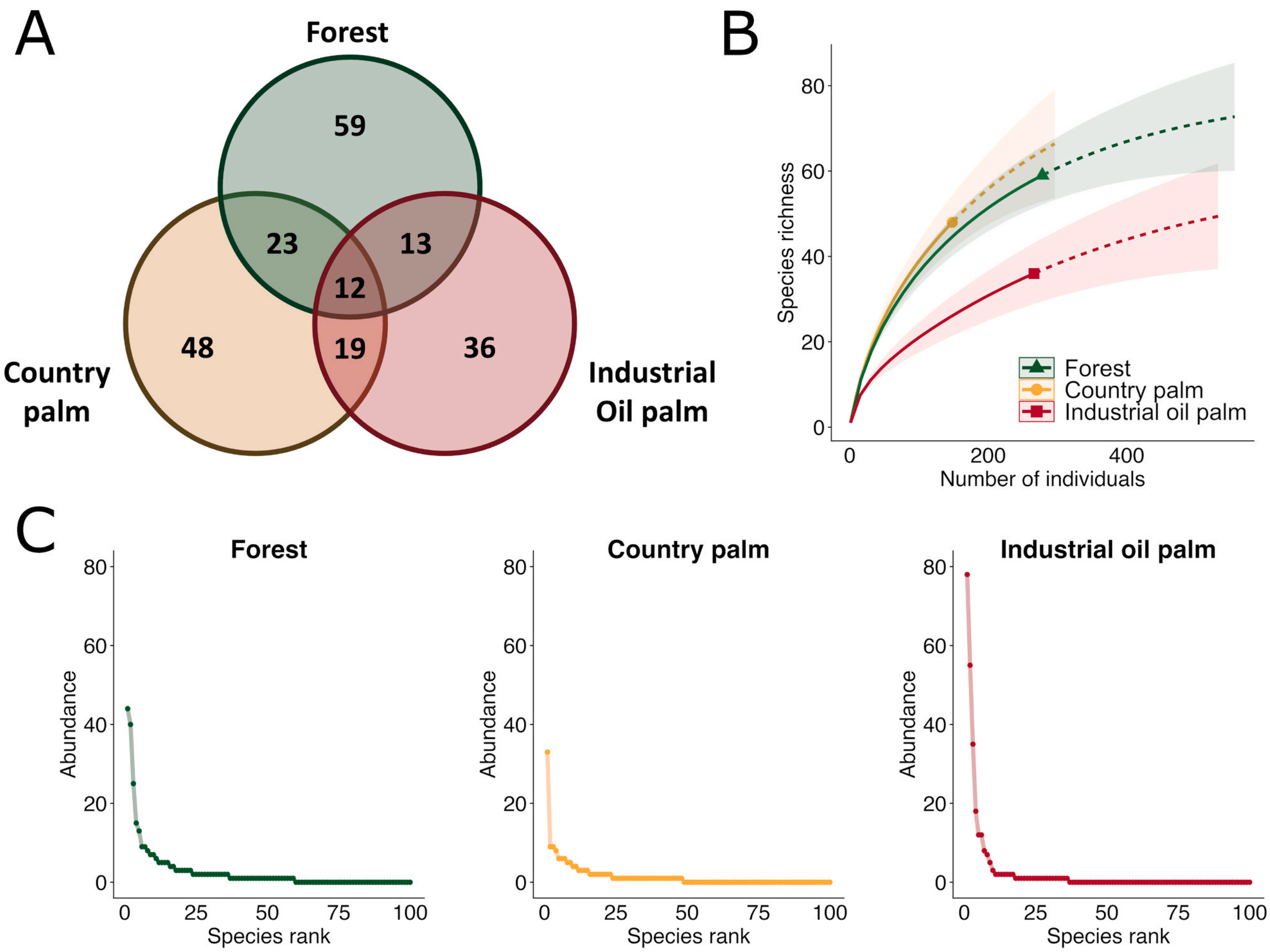

Fig. 2. Venn diagram showing (A) overlap of spider species between systems, (B) species accumulation curves, and (C) rank abundance curves for spiders in the understory across forest, country palm, and industrial oil palm systems. For (A), numbers in circles indicate the total number of species found in that system, and numbers in areas of circle overlap indicate the number of shared species across systems. For (B), we plotted both interpolated (solid line) and extrapolated (dotted line) curves. We extrapolated to double the number of collected individuals (following Chao et al., 2014; Gotelli and Colwell, 2001). For (C), points indicate individual species (N = 100 total). Axes are consistent for comparison across sub-plots.

were driven by significant changes in the abundance of two araneids (Araneidae sp. 3, *Gasteracantha curvispina*), one mysmenid (Mysmenidae sp. 1), two pholcids (Pholcidae sp. 2, Pholcidae sp. 3), two tetragnathids (Tetragnathidae sp. 1, Tetragnathidae sp. 2), two theridiids (Argyrodes sp. 2, Theridiidae sp. 12), and two theridiosomatids (Theridiosomatidae sp. 1, Theridiosomatidae sp. 2) ($P_{Univariate} < 0.05$).

3.2. Impacts of traditional and industrial approaches to oil palm cultivation on spider web-building

We collected web-building and prey capture data from 1015 orb web-building spiders, including 256 spiders in forest, 232 spiders in country palm, and 527 spiders in industrial oil palm. We found differences in the average web area ($LRT_{System} = 15.424$, $P_{System} < 0.001$), total web area ($LRT_{System} = 31.687$, $P_{System} < 0.001$), and standard deviation of web area ($LRT_{System} = 9.743$, $P_{System} < 0.008$) of orb web-building spiders across forest, country palm, and industrial oil palm systems (Fig. 4A-C). Post-hoc analyses showed that the average web area in industrial oil palm (232.6 ± 24.7 cm^2) was 2.3 times greater than in country palm (103.2 ± 14.1 cm^2) ($P_{Comparison} < 0.001$), and that the average web area in forest (171.8 ± 27.5 cm^2) was 1.7 times greater than in country palm ($P_{Comparison} = 0.032$) (Fig. 4A). The total web area in industrial oil palm (6947.4 ± 953.4 cm^2) was 3.1 and 5.2 times greater, respectively, than in forest (2235.9 ± 389.2 cm^2) ($P_{Comparison} < 0.001$) and country palm (1343.6 ± 273.2 cm^2) ($P_{Comparison} < 0.001$) (Fig. 4B). The standard deviation of web area in industrial oil palm (280.3 ± 30.9 cm^2) was 2.0 times greater than in country palm (137.6 ± 29.3 cm^2) ($P_{Comparison} = 0.004$) (Fig. 4C).

3.3. Impacts of traditional and industrial approaches to oil palm cultivation on spider prey capture

We found differences in the average captured prey ($LRT_{System} = 6.295$, $P_{System} = 0.043$), total captured prey ($LRT_{System} = 31.459$, $P_{System} < 0.001$), and proportion of webs with captured prey ($LRT_{System} = 13.899$, $P_{System} < 0.001$), but not the standard deviation of captured prey ($LRT_{System} = 1.473$, $P_{System} = 0.479$), of orb-web building spiders across forest, country palm, and industrial oil palm systems (Fig. 5A-D). Parametric bootstrapping upheld our average captured prey findings ($P_{Bootstrapped} = 0.049$). Post-hoc analyses showed that average captured prey in industrial oil palm (75.3 ± 7.1) was 1.8 times greater than in country palm (42.4 ± 7.7) ($P_{Comparison} = 0.025$) (Fig. 5A). Total captured prey in industrial oil palm (22.7 ± 4.1) was 2.9 and 4.1 times greater, respectively, than in forest (7.9 ± 1.1) ($P_{Comparison} < 0.001$) and country palm (5.6 ± 1.3) ($P_{Comparison} < 0.001$) (Fig. 5B). The proportion of webs with captured prey in industrial oil palm (19 ± 2.0 %) was 1.5 and 2.7 times greater, respectively, than in forest (13 ± 3.0 %) ($P_{Comparison} = 0.024$) and in country palm (7.0 ± 2.0 %) ($P_{Comparison} < 0.001$) (Fig. 5D).

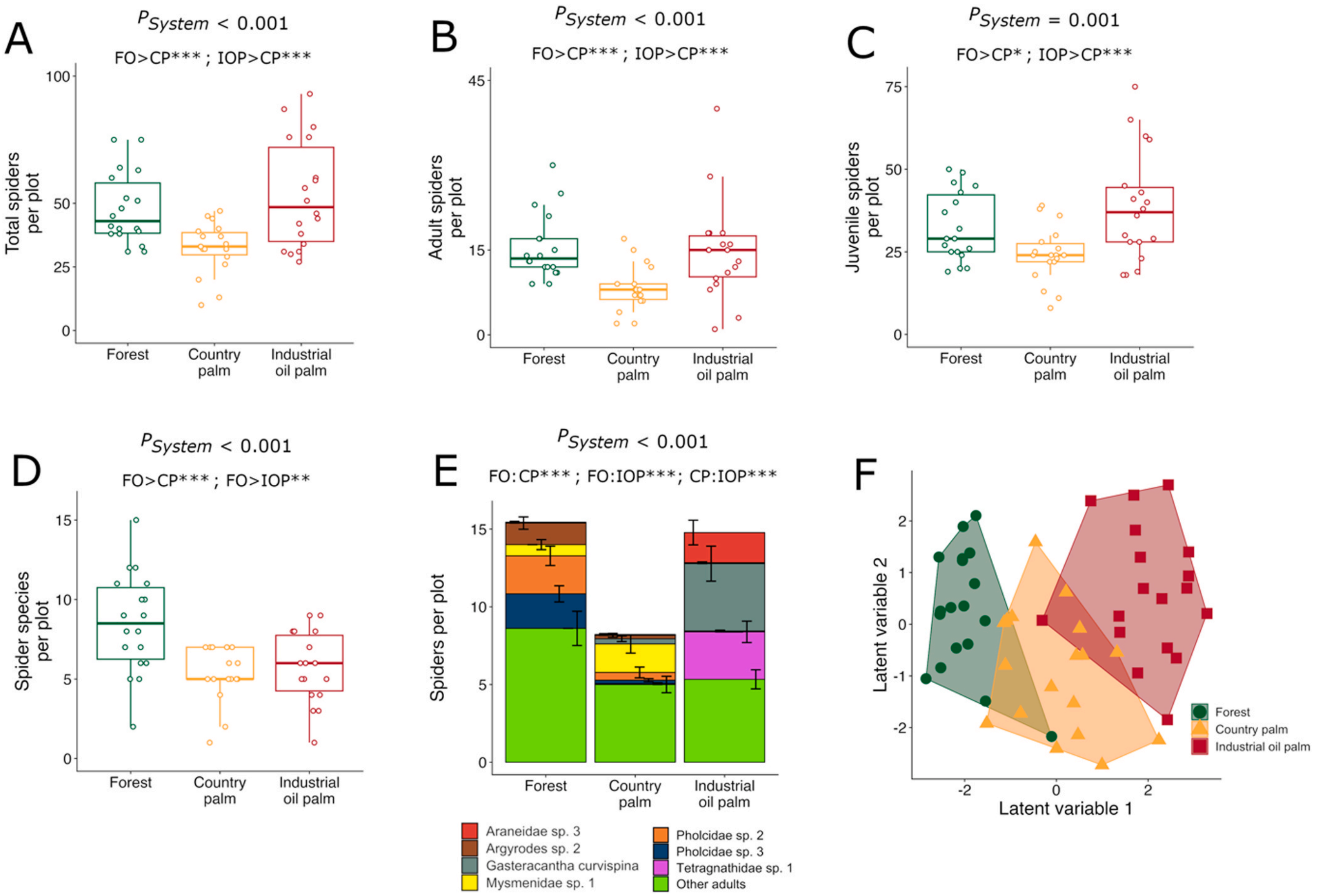

Fig. 3. Differences in the abundance of (A) all spiders, (B) adults-only, and (C) juveniles-only; (D) spider species richness; and (E,F) spider species-level community composition in the understory across studied systems (*Forest, Country palm, Industrial oil palm*). For (A-E), the effect of *System* on each response (determined using LRTs) and results of pairwise post-hoc testing (Tukey all-pair comparison tests, adjusted using a Bonferroni correction) are indicated above each plot: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$; FO = Forest, CP = Country palm, IOP = Industrial oil palm. For (A – D), boxplots show median (horizontal crossbar) and interquartile ranges, and circles show per-plot values. For (E), error bars show the mean and standard error. We include (F) as an additional visualisation of the species-level community composition. For (F), points represent the posterior medians of our GLLVM. We drew hulls around points of the same system to aid visualisation.

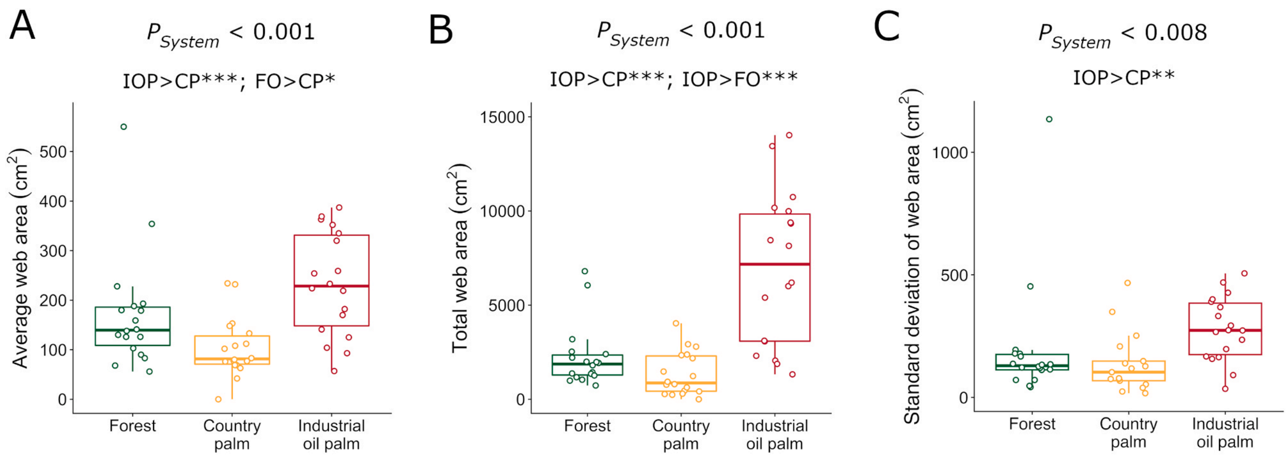

Fig. 4. Differences in the (A) average web area, (B) total web area, and (C) standard deviation of web area of orb web-building spiders in the understory across studied systems (*Forest, Country palm, Industrial oil palm*). Boxplots show median (horizontal crossbar) and interquartile ranges, and circles show per-plot values. The effect of *System* on each response (determined using LRTs) and results of pairwise post-hoc testing (Tukey all-pair comparison tests, adjusted using a Bonferroni correction) are indicated above each plot: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$; FO = Forest, CP = Country palm, IOP = Industrial oil palm.

Our sensitivity analysis, in which we examined changes in captured prey relative to web area in each system, showed that land use change did not affect captured prey per web area ($LRT_{System} = 0.178$, $P_{System} = 0.915$) (Supplementary Figure 1). This indicates that differences in captured prey were related to differences in total webbing across systems, rather than level of prey capture per unit of web area.

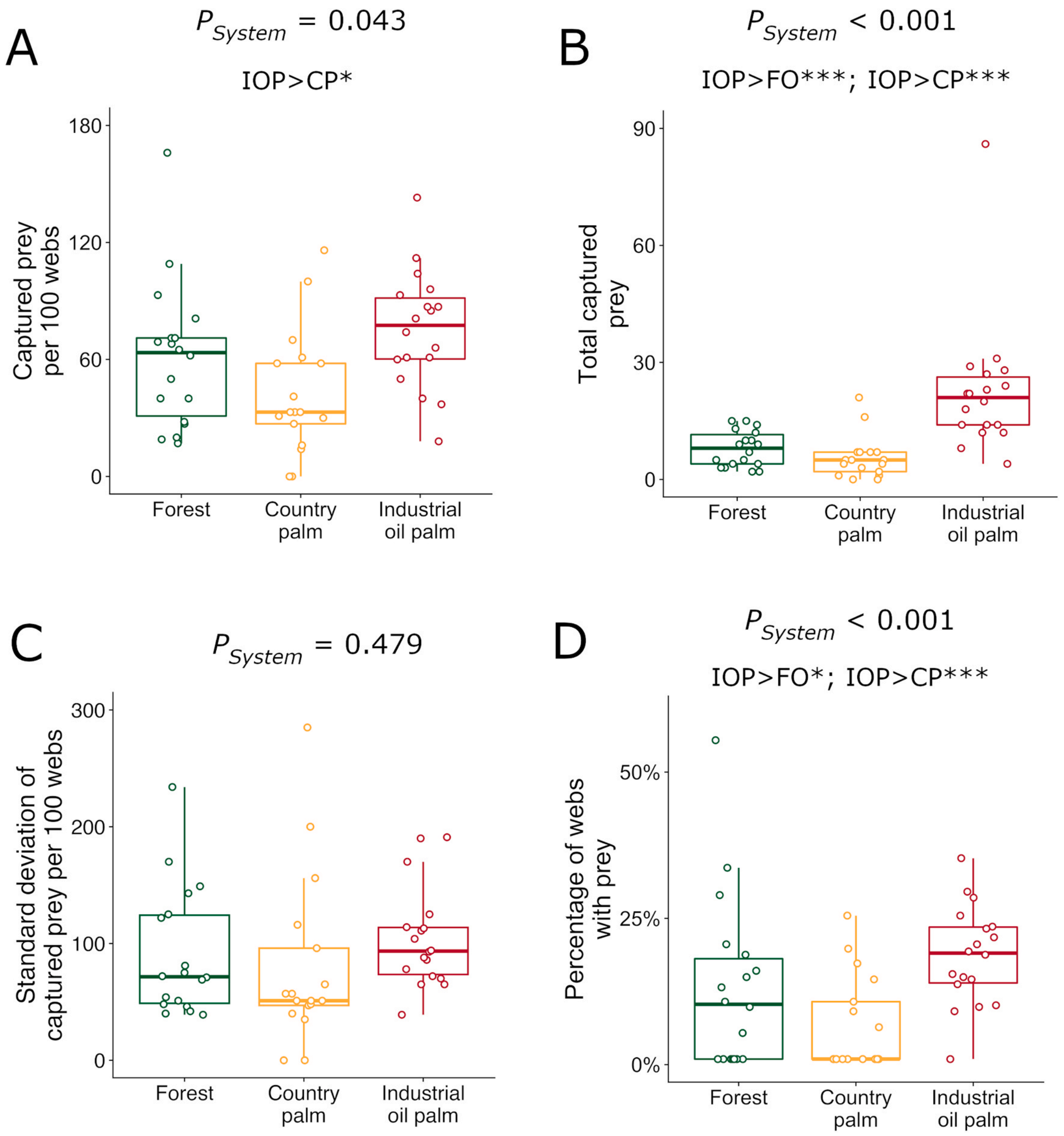

Fig. 5. Differences in the (A) average captured prey, (B) total captured prey, (C) standard deviation of captured prey, and (D) proportion of webs with captured prey of orb web-building spiders in the understory across studied systems (*Forest, Country palm, Industrial oil palm*). Boxplots show median (horizontal crossbar) and interquartile ranges, and circles show per-plot values. The effect of *System* on each response (determined using LRTs) and results of pairwise post-hoc testing (Tukey all-pair comparison tests, adjusted using a Bonferroni correction) are indicated above each plot: ****P* < *0.001*, ***P* < *0.01*, **P* < *0.05*; FO = Forest, CP = Country palm, IOP = Industrial oil palm.

4. Discussion

In this study, we assessed differences in the biodiversity, web-building, and prey capture of spiders in the understory across rainforest and two styles of oil palm cultivation (fallowed farmland with wild-growing oil palms, which local people manage and harvest, ‘country palm’; and industrial oil palm farms) in Sinoe County, Liberia. Across systems, we found 2408 spiders and 100 spider species. Spiders were relatively abundant in all systems, although they were least abundant in country palm. We also found more spider species in rainforest relative to country palm and industrial oil palm, and differences in species-level community composition between all systems, owing to changes in the relative abundance of several spider species. Focussing on orb web-building spiders, we found the greatest average web area, total web area, and standard deviation of web area in industrial oil palm. Owing to this high amount of webbing, industrial oil palm had the highest levels of average captured prey, total captured prey, and proportion of webs with captured prey.

4.1. Effects of oil palm cultivation on spider biodiversity

We found that rainforest (the locally native habitat) had more spider species in total, and on average, than country palm and industrial oil palm, although our species accumulation curves indicated that the total number of species in rainforest and country palm was likely similar. The higher number of spider species that we detected in rainforest, relative to country palm and industrial oil palm, is probably due to differences in environmental conditions across systems. In comparison to oil palm systems, rainforests support more diverse and complex communities of understory and overstory vegetation and are cooler and more humid (Luskin and Potts, 2011; Meijide et al., 2018; Rembold et al., 2017). These environmental changes may affect spiders—especially those in the understory—because they depend on speciose and structurally complex vegetation for reproduction, web-building, and prey capture, and require cool and humid microclimates to prevent desiccation (which threatens spiders more than, for instance, insects, owing to spiders having only semi-hardened exoskeletons) (Diehl et al., 2013). The higher number of spider species in rainforest may also be attributed to differences in insect prey availability between systems. Work in Malaysia has shown that the abundance and biomass of insects, which form the bulk of spider diet, is substantially lower in oil palm than rainforest systems (Turner and Foster, 2009). Although spiders are mostly generalist predators, with spider body size largely dictating which prey are eaten (Nentwig, 1982), many species have different levels of specificity to certain and variable prey items (e.g., Pekár and Toft, 2015), and therefore effects of rainforest conversion on insects may have secondary impacts on spiders. Our findings echo studies from Southeast Asia, which found that rainforest conversion to smallholder oil palm plantations caused 57–98 % declines in the species richness of ground-dwelling spiders (Potapov et al., 2020), although another study in the same sites found no effects of rainforest conversion on the species richness of salticids in the canopy (Junggebauer et al., 2021). This indicates that land use change has microhabitat-specific effects on spider biodiversity. Future studies in other microhabitats are needed to quantify the impacts of converting rainforest to oil palm systems on spiders in West Africa. Overall, our findings, and those of others (e.g., (Junggebauer et al., 2021; Potapov et al., 2020)), indicate that tropical rainforests are an irreplaceable habitat for spiders, relative to oil palm systems, mimicking patterns observed more generally across taxonomic groups (Drescher et al., 2016; Foster et al., 2011).

Rainforest did not consistently support higher abundances of all spider species, leading to differences in community composition across systems. The spider community in rainforest was characterised by a relatively high abundance of a theridiid species (Argyrodes sp. 2, ~ 9 % of all adult spiders in rainforest) and two pholcid species (Pholcidae sp. 2 and Pholcidae sp. 3, ~ 16 % and ~ 14 % of all adult spiders in rainforest, respectively); the spider community in country palm was characterised by a high abundance of a mysmenid species (Mysmenidae sp. 1, ~ 22 % of all adult spiders in country palm); and the spider community in industrial oil palm had high abundances of two araneids (Araneidae sp. 3 and *Gasteracantha curvispina*, ~ 14 % and ~ 30 % of all adult spiders in industrial oil palm, respectively) and a tetragnathid (Tetragnathidae sp. 1, ~ 21 % of all adult spiders in industrial oil palm). Our findings therefore demonstrate that there are clear “winning” and “losing” spider species that arise from rainforest conversion to oil palm. While very little is known about the ecology of spider species in West Africa and particularly Liberia (Cardoso et al., 2019), it is likely that spider species found abundantly in rainforest, but not in country palm and industrial oil palm (i.e., “losers” when rainforest is converted to alternative land uses) are specialist species that can only survive in specific environmental conditions, such as areas of high humidity, that do not exist in country palm and industrial oil palm systems. Conversely, it is likely that spider species found abundantly in industrial oil palm (i.e., “winners” when oil palm farms are established) are generalists that can survive multiple disturbance events and can tolerate a wide variety of environmental conditions. For example, the most abundant spider that we found in industrial oil palm was *Gasteracantha curvispina* ($n = 78$; a species found widely across Central and West Africa (World Spider Catalog, 2023)), and Gastercantha spp. inhabit disturbed landscapes across the tropics and sub-tropics worldwide (World Spider Catalog, 2023). Whilst not studied explicitly in spiders, these phenomena have been observed in other invertebrate groups such as ants (Fayle et al., 2015). Although generalist spiders may be less important than rainforest specialists from a conservation perspective, they can be functionally important in agricultural systems and therefore efforts should be made to increase their abundance and biodiversity within oil palm. For instance, spiders are important providers of pest control services and can therefore positively affect crop yields (Michalko et al., 2019).

In comparison to industrial oil palm, we found that country palm was more like rainforest in terms of species richness and community composition. Indeed, our species accumulation curves indicated that country palm likely supported a similar number of total spider species as rainforest, although average species richness in country palm was lower than in rainforest. In addition, our composition analyses showed country palm to sit between rainforest and industrial oil palm. The greater similarity between country palm and rainforest, relative to industrial oil palm and rainforest, is not surprising. In comparison to industrial oil palm, vegetation structure and microclimate in country palm is more similar to that in rainforest (Pashkevich et al., In Review), owing in part to industrial oil palm managers regularly clearing understory vegetation in farms to allow easier access for harvesters. Conditions in country palm may suit the habitat requirements of a wider variety of spider species, including some rainforest specialists. Further, our country palm plots were closer to rainforest areas than industrial oil palm (Pashkevich et al., 2024), possibly allowing spillover of rainforest spider species into country palm (Lucey and Hill, 2012). It is also noteworthy that most disturbance in country palm occurs as farms are established, and so potentially more species can persist and then recover as country palm systems regenerate after farmers plant their crops. In comparison, disturbance in industrial oil palm is continuous owing to high-intensity management practices that include regular application of chemical fertilisers, pesticides, or herbicides, which potentially negatively affect some spider species (Spear et al., 2018). Intensive management has previously been shown to select for generalist spider species (Pashkevich et al., 2021), and therefore the lower levels of management in country palm are likely to allow a greater variety of spiders to persist, including some species that are best supported in rainforest. It is noteworthy that, although country palm had a more similar spider community and total species richness than industrial oil palm relative to rainforest, the average abundance of all spiders, adults only, and juveniles only was lower in country palm than rainforest or industrial oil palm. The relatively low abundance of spiders in country palm is likely owing to the dense vegetation found in this system, which exceeded the density of vegetation found in rainforest and industrial oil palm (Unpublished results). Our country palm plots are community-managed farmlands that had been left fallow for 2–30 years before survey (Pashkevich et al., 2024). Natural regeneration occurred within these areas, resulting in thick vegetation (‘low bush’) and leaving minimal space for spiders to spin their webs. In comparison, in the rainforest, spiders could build their webs between trees and mid- and understory vegetation. In industrial oil palm, there is relatively little understory vegetation owing to heavy application of herbicides, allowing spiders to build their webs between palms in relatively high densities (Pashkevich et al., 2021). We acknowledge that greater visibility in industrial oil palm—owing to the relatively low levels of understory vegetation and more open canopy (Pashkevich et al., 2024)—may have made detection of spiders easier, potentially inflating relative counts of spiders in this system. To mitigate detectability bias caused by differences in canopy openness and light levels, we used a headtorch while sampling.

4.2. Effects of oil palm cultivation on spider web-building and prey capture

Our focussed analyses on orb web-building spiders (families Araneidae, Tetragnathidae, Theridiosomatidae, and Uloboridae) indicated that there was consistently more webbing and, on average, more prey captured in industrial oil palm, relative to rainforest and country palm. This suggests that conversion of rainforest to oil palm affects the functioning of spiders, in addition to biodiversity. As the abundance of all spiders, adults only, and juveniles only did not differ between rainforest and industrial oil palm systems, our findings indicate that conversion of rainforest to oil palm selects for species that spin larger orb webs. This is supported by our biodiversity surveys, which showed that the most abundant spiders in industrial oil palm were relatively large species that spin correspondingly large webs (e.g., *Gasteracantha curvispina*, for which female body length is approximately 10 mm). We also found a greater proportion of webs with captured prey in industrial oil palm, relative to rainforest and country palm, indicating that insect prey is available in this system, and therefore that prey availability is likely not the determining factor for which spider species are "winners" and "losers" when rainforest is converted to oil palm. This point is further supported by our sensitivity analysis, in which we showed that differences in captured prey between systems were likely explained by cross-system differences in total webbing rather than differences in prey density.

The relatively high rates of prey capture in all systems indicate that spiders are an important mesopredator in rainforest, country palm, and industrial oil palm systems in Southeast Liberia. In country palm and industrial oil palm, spider-mediated predation could have a positive impact on oil palm growth and yield, as spiders in these systems may be consuming oil palm pests. The major pests in West African oil palm systems are *Parasa pallida* and *Parasa viridissima* (also called *Latoia pallida* and *Latoia viridissima*), both slug moths, which defoliate oil palm fronds as larvae (Fedière et al., 1990). It is possible that adult moths are captured in spider webs, therefore helping to control pest abundance, although we are aware of no studies that have explicitly shown this, and we did not quantify this relationship in this study. Further, spiders may predate larvae of these species, which are approximately 3.5 – 36.0 mm in length (depending on whether larvae are young or mature) (Ukeh, 2007), and therefore well within the size range of potential prey for many of the spider species we captured (Rusch et al., 2015), and inhabit the understory microhabitat that we studied (Igbinosa, 1985). Industrial oil palm managers in West Africa typically control populations of *P. pallida* and *P. viridissima* by spraying chemical pesticides, although Fedière et al. (1990) has suggested using a virus to control these pests. Our findings indicate that enhancing spider abundance and biodiversity could also be an effective strategy for controlling these pest species, and such an approach could form an important component of integrated pest management, which aims to improve levels of pest control by enhancing the abundance of natural enemies, such as spiders, rather than using chemical pesticides (Hinsch & Turner, 2018).

It is noteworthy that we only assessed differences in web-building and prey capture in orb web-building spiders (families Araneidae, Tetragnathidae, Theridiosomatidae, and Uloboridae), since it is easy to measure and count prey within their webs. While these families were abundant in all systems we studied, spiders from other web-building families (e.g., Pholcidae and Theridiidae, which spin three-dimensional tangle webs) were relatively more abundant in rainforest plots and, during fieldwork, we noticed a high rate of prey capture in these webs. Therefore, our web-building and prey capture findings are specific only to orb web-building spiders, and caution should be taken when applying them to overall spider communities.

4.3. *Implications for conservation and management*

Our findings have clear implications for conservation and management. First, our findings demonstrate that rainforests are an irreplaceable habitat for spiders in Liberia. Liberia currently has the highest density of rainforest in West Africa, but rates of deforestation for agriculture, mining, and logging purposes are increasing substantially (Davis et al., 2020). Increased efforts are needed to protect rainforest whenever possible. If rainforest is converted to an alternative land use system (e.g., agriculture), we recommend conserving fragments of rainforest within the landscape, as this could mitigate some of the ecological impacts of rainforest loss, especially for smaller and more mobile taxa such as spiders (Lucey et al., 2014; Scriven et al., 2019). For instance, in the industrial oil palm farms in which we worked, fragments of rainforest have been conserved along rivers ("riparian buffers") and in culturally important areas (e.g., where towns used to be, and therefore where the ancestors of local people historically lived). Previous studies in Southeast Asia have indicated that conservation of riparian buffers and other rainforest fragments can mitigate the ecological impacts of oil palm cultivation (Deere et al., 2022; Lucey et al., 2014; Scriven et al., 2019), although conserving rainforest fragments is not a panacea for the overall ecological impacts of rainforest loss.

To our knowledge, our study is the first to examine spider communities in Liberia, sampling in both reference (i.e., rainforest) and alternative (i.e., country palm and industrial oil palm) ecosystems. Indeed, our study is one of only a few published ecological studies in Liberia since its civil wars (1989–2003) (Pashkevich et al., 2024). The spiders we collected therefore provide an important baseline ecological dataset that could be used for various purposes. For instance, future survey work in Liberia can use the spider species that we found only in rainforest as ecological indicators of intact or successfully-restored habitat. Similarly, our sampling forms an important temporal dataset, to which future surveys can be compared to assess how climate change in West Africa is affecting invertebrate communities. Our collected spiders, one of the only invertebrate collections from Liberia existing worldwide, are stored at the University Museum of Zoology Cambridge with permission from the Forestry Development Authority of the Government of Liberia, with whom we are progressing conversations regarding the repatriation of a voucher series. We are also working on a photo series of the collection, which will be made available freely online, and we welcome contact from researchers who would like to use these specimens for future research purposes.

Our findings have clear implications for management within oil palm landscapes. We found that understory vegetation is a valuable habitat for spiders. If oil palm managers aim to increase the biodiversity of natural enemies, such as spiders, which may be critical to integrated pest management schemes and therefore oil palm yields (Hinsch & Turner, 2018; Nurdiansyah et al., 2016), efforts should be taken to maintain or improve levels of understory vegetation diversity and complexity within oil palm landscapes. Currently, in the industrial oil palm farms in which our study was carried out, herbicides are applied liberally to control understory vegetation and prevent understory species from competing with oil palms for nutrients and water (Pashkevich et al., 2024). Previous studies have indicated the value of retaining complex understory vegetation for spiders and other invertebrate taxa. For instance, in Indonesia, retaining understory vegetation in oil palm plantations was shown to increase the density of *Argyrodes miniaceus* (Doleschall, 1857) in Nephila spp. webs (Spear et al., 2018), although another study found that the benefits of increasing understory vegetation complexity for spiders in the canopy and on the ground were limited (Pashkevich et al., 2022). Managing for increased understory vegetation complexity could lead to overall increases in biodiversity and functioning in oil palm landscapes (Luke et al., 2020).

Oil palm in Sinoe County is cultivated in two main ways: from wild-growing palms in areas being actively or previously farmed by local people ('country palm') and industrial oil palm farms. Our findings indicate that industrial oil palm farms support more spider individuals, but that country palm supports spider communities that are more similar to those in rainforest. Although comparable oil palm yield data between country palm and industrial oil palm systems are not widely available, it is very likely that industrial oil palm has substantially higher yield than country palm, owing to the seed stock used and high rates of application of fertilisers (Corley and Tinker, 2016). Our study does not indicate whether a traditional or industrial cultivation style is superior to the other, but suggests that country palm and industrial oil palm systems offer different trade-offs between conservation and palm oil yields. Efforts are needed to better quantify these trade-offs, and to determine how much oil palm cultivation can expand in Liberia without sacrificing the integrity of its rainforest ecosystems, with implications for traditional land management approaches and livelihoods. Understanding these trade-offs is of paramount importance to conservation of West African rainforests, while ensuring that food security goals are met in West Africa and worldwide.

CRediT authorship contribution statement

Ari Saputra: Data curation, Conceptualization. **Michael David Pashkevich:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rudy Widodo:** Conceptualization. **Brogan Pett:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Edgar Turner:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Cicely Marshall:** Writing – review & editing, Methodology, Investigation, Data curation. **Jean-Pierre Caliman:** Writing – review & editing, Conceptualization. **Benedictus Freeman:** Writing – review & editing, Conceptualization. **Marshall Guahn:** Data curation. **Peter Hadfield:** Data curation, Conceptualization. **Matthew Hendren:** Data curation. **Morris Jah:** Data curation. **Tiecanna Jones:** Data curation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Michael Pashkevich reports financial support was provided by Biotechnology and Biological Sciences Research Council. Michael Pashkevich reports financial support was provided by Cambridge Philosophical Society. Cicely Marshall reports financial support was provided by University of Cambridge King's College. Matthew Hendren reports financial support was provided by Natural Environment Research Council. Michael Pashkevich reports administrative support was provided by Government of the Republic of Liberia. Michael Pashkevich reports administrative support and travel were provided by Golden Veroleum Liberia. Rudy H. Widodo reports a relationship with Golden Veroleum Liberia that includes: employment. Morris T. Jah reports a relationship with Government of the Republic of Liberia that includes: employment. Ari Saputra reports a relationship with Golden Veroleum Liberia that includes: employment. Peter M. Hadfield reports a relationship with Ecology Solutions Ltd. that includes: employment. Jean-Pierre Caliman reports a relationship with Sinar Mas Group that includes: employment. We are grateful to the local communities of Sinoe County, the Forestry Development Authority (FDA) and Ministry of Agriculture (MoA) of the Government of Liberia, Golden Veroleum Liberia (GVL), and Golden Agri Resources for permission to carry out research within our study systems. We are very appreciative of all local people in Sinoe County who assisted with fieldwork, and particularly Mr. Samuel Jayswen, Mr. Jeremiah Kun, Mr. Sam Kandie, Mr. Daniel Koffa, Mr. Benedict Manewah, Mr. Jimmy Tue, and Mr. Josiah Tueleh. MDP thanks the Marshall Sherfield Foundation, Biotechnology and Biological Sciences Research Council Impact Acceleration Award (BBSRC IAA, award number BB/S506710/1), St Edmunds College (University of Cambridge), and Cambridge Philosophical Society for funding. CAMM thanks King's College Cambridge for funding. MTH was funded by NERC C-CLEAR Research Experience Placement (REP) funding while working on this project. We thank the Government of Liberia for permission to conduct our research (Republic of Liberia Business Visa #420), and the FDA for permission to collect (permit number: MD/022/2022/-4) and export (permit number: MD/048/2022/-1) spiders. Co-Authors with an affiliation to Sinar Mas Agro Resources and Technology Research Institute (SMARTRI), Golden Veroleum Liberia, or the Forestry Development Authority of the Government of Liberia were employed by their respective institutions while this work was conducted. University of Cambridge retained all intellectual property rights, and no attempts were made by any co-authors or their respective organisations to influence the work or its findings unduly. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data availability

Data are available on the University of Cambridge Online Digital Repository: https://doi.org/10.17863/CAM.109073.

Acknowledgements

We are grateful to the local communities of Sinoe County, the Forestry Development Authority (FDA) and Ministry of Agriculture (MoA) of the Government of Liberia, Golden Veroleum Liberia (GVL), and Golden Agri Resources for permission to carry out research within our study systems. We are very appreciative of all local people in Sinoe County who assisted with fieldwork, and particularly Mr. Samuel Jayswen, Mr. Nehemiah Koon, Mr. Sam Kandie, Mr. Daniel Koffa, Mr. Benedict Manewah, Mr. Jimmy Tue, and Mr. Josiah Tuolee. MDP thanks the Marshall Sherfield Foundation, Biotechnology and Biological Sciences Research Council Impact Acceleration Award (BBSRC IAA, award number BB/S506710/1), St Edmunds College (University of Cambridge), and Cambridge Philosophical Society for funding. CAMM thanks King's College Cambridge for funding. MTH was funded by NERC C-CLEAR Research Experience Placement (REP) funding while working on this project. We thank the Government of Liberia for permission to conduct our research (Republic of Liberia Business Visa #420), and the FDA for permission to collect (permit number: MD/022/2022/-4) and export (permit number: MD/048/2022/-1) spiders.

Author contributions

MDP led data collection (with assistance from CAMM, PMH, MTJ, MMG, TJ, and AS), statistical analyses, and writing of the manuscript. BP identified the spiders (assisted by MTH). MDP, CAMM, J-PC, BF, AS, RHW, and ECT helped to design and facilitate the larger administration of the SOPWA Project, in which this study was based. All authors approved the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109102.

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