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Traditional and industrial approaches to oil palm cultivation alter the biodiversity of ground-dwelling arthropods in Liberia (West Africa)

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ABSTRACT

Oil palm cultivation is vital to global food security and economically important to farmers. However, the rapid expansion of oil palm plantations has caused large-scale deforestation in the tropics and, consequently, biodiversity loss and changes in ecosystem functioning. Oil palm is primarily cultivated in Southeast Asia, where the ecological impacts of production have been studied extensively. It is also grown in West Africa, using traditional and industrial methods of cultivation. However, in comparison to Southeast Asia, relatively little research on the impacts of oil palm cultivation in West Africa has occurred. Working in the framework of the Sustainable Oil Palm in West Africa (SOPWA) Project (Sinoe County, Liberia), we investigated differences in the biodiversity of ground-dwelling arthropods across rainforest (the regional natural habitat) and oil palm systems cultivated under traditional (called "country palm") and industrial management. We sampled arthropods with pitfall traps (160 retrieved) across 54 monitoring plots in rainforest, country palm, and industrial oil palm. We found no differences in total arthropod abundance across systems, but we did find changes in arthropod order-level community composition, driven by differences in the relative abundance of Araneae, Collembola, Dermaptera, and Diptera. We conducted focused morphospecies-level analyses on spiders, owing to their key roles as predators within tropical agricultural systems, and to determine if our order-level findings held true at increased taxonomic resolution. Our spider analyses indicated that country palm supported the greatest number of spider individuals and species, and that all systems supported distinct spider assemblages. Our findings have implications for both arthropod conservation and oil palm productivity, owing to the important ecosystem functions (e.g., pest control) that many arthropods provide. Future research should investigate whether changes in on-farm management practices influence arthropod communities – and the ecosystem functions they support – in West Africa.

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1. Introduction

Palm oil, the most traded vegetable oil globally, is made from the fruits of the oil palm (*Elaeis guineensis* Jacq). Global palm oil production is increasing rapidly. For instance, from 2000 to 2020, production more than tripled (22.23 Mt to 75.88 Mt), and oil palm plantation area doubled (10.40 Mha to 21 Mha) (Descals et al., 2021; Ritchie and Roser, 2021). Oil palm agriculture is vital to global food and fuel security, and can benefit the income and livelihoods of small-scale farmers and local communities (Chrisendo et al., 2022; Khatun et al., 2020; Nurfatriani et al., 2022). For instance, a study in Indonesia found that cultivating oil palm was associated with improved nutrition, education, living conditions, and human capital formation in smallholder farm households (Chrisendo et al., 2022). However, oil palm agriculture has also dramatically affected tropical ecosystems (Barnes et al., 2014; Koh and Wilcove, 2008; Vijay et al., 2016), as increases in production have occurred mainly at the expense of tropical rainforest habitats and, to a lesser extent, savanna and peatlands (Fleiss et al., 2022; Gibbs et al., 2010; Vijay et al., 2016; Warren-Thomas et al., 2022). Conversion of natural habitat to oil palm reduces vegetation structural complexity and diversity, and alters microclimate (Hardwick et al., 2015; Luskin and Potts, 2011; Pashkevich et al., 2024a; Williamson et al., 2021), resulting in lower levels of biodiversity across taxonomic groups (e.g., mammals (Bernard et al., 2016; Sodhi et al., 2009; Yue et al., 2015), birds (Azhar et al., 2011; Hamer et al., 2021; Nájera and Simonetti, 2010), and arthropods (Alonso-Rodríguez et al., 2017; Mumme et al., 2015; Turner and Foster, 2009)) and changing levels of ecosystem functioning (Barnes et al., 2014; Dislich et al., 2017).

The majority of oil palm is grown in Southeast Asia, where the ecological impacts of cultivation have been studied extensively (Popkin et al., 2022; Reiss-Woolever et al., 2021). However, oil palm agriculture is also expanding in other producing regions, yet relatively little research has focused on the potential societal and ecological impacts of associated land use changes (Pashkevich et al., 2024a; Reiss-Woolever et al., 2021). For instance, in West Africa (oil palm's native home), oil palm cultivation is increasing in many countries, but studies on the environmental impacts of cultivation in this region are relatively rare (Pashkevich et al., 2024a; Reiss-Woolever et al., 2021). The impacts of industrial cultivation in West Africa may vary from those observed in Asia and South America, since oil palm is native to West Africa and therefore has co-evolved with other species (in other regions, it has been introduced, and its cultivation may therefore have greater ecological impacts). Further, many West African people practice locally unique cultivation practices, including harvesting of wild-growing palms, which grow naturally in areas of low-lying rainforest. These palms are often retained when new smallholder farms are established, in which other crops such as cassava, banana, cucumber, okra, and pepper are grown for subsistence purposes (Pashkevich et al., 2024a). This small-scale production is in stark contrast to industrial expansion, which is also increasing in some parts of West Africa, and involves vast areas of rainforest being converted to oil palm monocultures (Descals et al., 2021; Paterson, 2021). These large-scale plantations are often established by foreign corporations and managed following strategies developed in Southeast Asia, including high application of inorganic fertilisers and herbicides (Davis et al., 2020; Pashkevich et al., 2024a).

Liberia is the third most-forested country in Africa and the most-forested (by percentage of land area) country in West Africa (Forest Carbon Partnership, 2019; Index Mundi, 2019). Liberia's tropical moist to hyperwet broadleaf forests comprise the majority of the remaining Upper Guinean Rainforest (Environmental Protection Agency Liberia, 2019; UNEP/GRID-Geneva, 2023), a Critical Region for Conservation, owing to the many endemic and threatened species that it contains (Marshall et al., 2016, 2022; Olson and Dinerstein, 2002; UNEP/GRID-Geneva, 2023; United States Agency for International Development, 2018). The rainforests are also important to the livelihoods of local people. For instance, people in Liberia use plants from the rainforest as sources of housing materials and medicines for treating malaria and other common diseases (Marshall and Hawthorne, 2012, 2013; Marshall et al., 2024). In comparison to surrounding countries, Liberia's rainforests are relatively undisturbed due to Liberia's historically small population and two civil wars (1989 – 1997, 1999 – 2003) and an Ebola outbreak (2013 – 2016) that halted large-scale land development for decades (Okoli et al., 2019; United Nations Development Programme, 2014). However, in recent years, large-scale land development (including for oil palm cultivation) in Liberia has occurred. This development has the potential to support local income, livelihoods and food security, but research is needed urgently to identify the ecological and socioeconomic impacts of this expansion, and to develop methods to cultivate oil palm more sustainably in this region (Pashkevich et al., 2024a).

Arthropods (here meaning insects, arachnids, and myriapods) are highly abundant and functionally important in most terrestrial habitats, including oil palm plantations (Cheong et al., 2010; Pashkevich et al., 2021). In oil palm landscapes, they provide vital ecosystem services that support yields. For example, ants predate on pests (Exélis et al., 2022; Offenberg, 2015), springtails and termites are decomposers that benefit soil fertility (Gray et al., 2014; Mumme et al., 2015), and a single species of beetle (*Elaeidobius kamerunicus* Faust, Coleoptera: Curculionidae) underpins pollination in industrial farmlands (Gintoron et al., 2023; Li et al., 2022). However, some arthropods can provide ecosystem disservices, such as bagworms (family: Psychidae) and slug moth caterpillars (family: Limacodidae; *Parasa* spp.), which damage palm fronds and reduce yields (Corley and Tinker, 2016). Arthropods are also prey for other fauna such as mammals, birds, reptiles, and amphibians, thus playing an important role in energy transfer from the lower to upper trophic levels (Deblauwe and Janssens, 2008; Mizsei et al., 2019; Rytkönen et al., 2019). Therefore, conservation of arthropods is vital for sustaining tropical biodiversity and oil palm productivity (Dislich et al., 2017; Turner and Hinsch, 2018). Despite this, in comparison to Southeast Asia, there have been relatively few studies on the impacts of oil palm expansion on arthropods in West Africa. Studies from Southeast Asia show that converting natural habitat to oil palm plantations negatively impacts arthropods (Ashton-Butt et al., 2019; Gray et al., 2016; Mumme et al., 2015; Nurdiansyah et al., 2016; Rizali, Karindah, et al., 2019; Turner and Foster, 2009). For instance, Lucey and Hill (2012) found that, compared to natural rainforest, the species richness of butterflies and ants decreased by 54 % and 25 % respectively in oil palm plantations in Sabah, Malaysia. These impacts are likely due to several factors, such as reductions in understory vegetation and hotter and drier conditions, that result when natural habitats are converted to oil palm plantations (Mumme et al., 2015; Turner and Foster, 2009).

In this study, we worked within the framework of the Sustainable Oil Palm in West Africa (SOPWA) Project (Pashkevich et al., 2024a) – a large-scale collaborative study focused on the socioecological benefits and consequences of oil palm cultivation in Sinoe County, Liberia – to study differences in ground-dwelling arthropod biodiversity across rainforest and oil palm systems being managed traditionally (called "country palm") and industrially. We had two main aims. First, considering all ground-dwelling arthropods at the order-level, we investigated whether oil palm systems support fewer arthropod individuals and different arthropod assemblages in comparison to rainforest. Second, considering spiders only, we investigated whether oil palm systems support fewer spider individuals, species, and different spider communities in comparison to rainforest. We conducted these focused spider analyses to investigate whether order-level findings were consistent at increased taxonomic resolution. We chose spiders specifically for three reasons. Firstly, they are predators of pests within tropical agricultural landscapes, including oil palm systems, and are therefore key for maintaining oil palm health and productivity (Pashkevich et al., 2022; Rosa et al., 2018; Spear et al., 2018). Second, studies have shown spiders to be an indicator taxon of the effects of converting rainforest to oil palm systems (Junggebauer et al., 2021;

Potapov et al., 2020; Ramos et al., 2022). Third, a previous study (Pashkevich et al., 2024b) investigated the response of spiders in understory vegetation to oil palm expansion in Liberia. As our current study focused on ground-dwelling spiders, it allows insights into how oil palm expansion may differently affect biodiversity across microhabitats. We did not identify all arthropods to species-level, owing to difficulties with the high diversity and poor taxonomic knowledge of West African arthropods. We hypothesised that: (1) Rainforests support more abundant and compositionally distinct arthropod communities than oil palm systems, and (2) Rainforests support more abundant, species rich, and compositionally distinct spider communities than oil palm systems. This research extends understanding of arthropod biodiversity in both rainforest and oil palm systems in West Africa, benefitting ongoing conservation efforts and providing important baseline data on arthropod biodiversity in an incredibly understudied tropical country. Our study is also a helpful comparison to similar studies in Southeast Asia (Mumme et al., 2015; Turner and Foster, 2009). The impacts of oil palm cultivation on arthropods are relevant to both conservation and food security goals, as many arthropod species support important ecosystem services – such as pest control and pollination – that support oil palm yield (Gérard et al., 2017; Li et al., 2019; Luke et al., 2020).

2. Materials and methods

2.1. Site

This study was conducted in Sinoe County, Liberia (5.135195 N, 9.078423 W; Fig. 1) in the framework of the Sustainable Oil Palm in West Africa (SOPWA) Project. The SOPWA Project is investigating the socioecological impacts of traditional and industrial approaches to oil palm production, using rainforest as a reference system (Pashkevich et al., 2024a). The industrial oil palm plantations are owned by Golden Veroleum Liberia (GVL), the largest oil palm producer in Liberia and a subsidiary company of Singapore-based Golden Agri-Resources (GAR). Sinoe Country has an average annual rainfall of 3600 mm and an annual average temperature of 25.7 °C (ranging from 20 – 31 °C) (Climate change Knowledge Portal, 2020; Climate-Data, 2023). The soil type is mainly latosol, a red soil which contains high iron and aluminium oxide content (Todd, 2016; United Nations Development Programme, 1970).

The SOPWA study design features study plots (50 ×50 m) in three different systems:

2.1.1. Forest

These plots are in GVL-owned old-growth lowland rainforest areas, which form part of the Upper Guinean Rainforest. There is no record of large-scale disturbance within these areas, but local people use them for cultural purposes, hunting bushmeat, and harvesting of non-timber forest products (NTFPs). As Sinoe County has the highest per-county forest cover in Liberia (about 90 % of Sinoe County is forest; Forest Carbon Partnership, 2019), forest is the ideal pre-oil palm reference habitat for this study.

2.1.2. Country palm

These plots are in traditional smallholder farms owned by local people who live in nearby villages. At the time of sampling, each plot had been farmed at least 2 years before the study began (range: 2 – 30

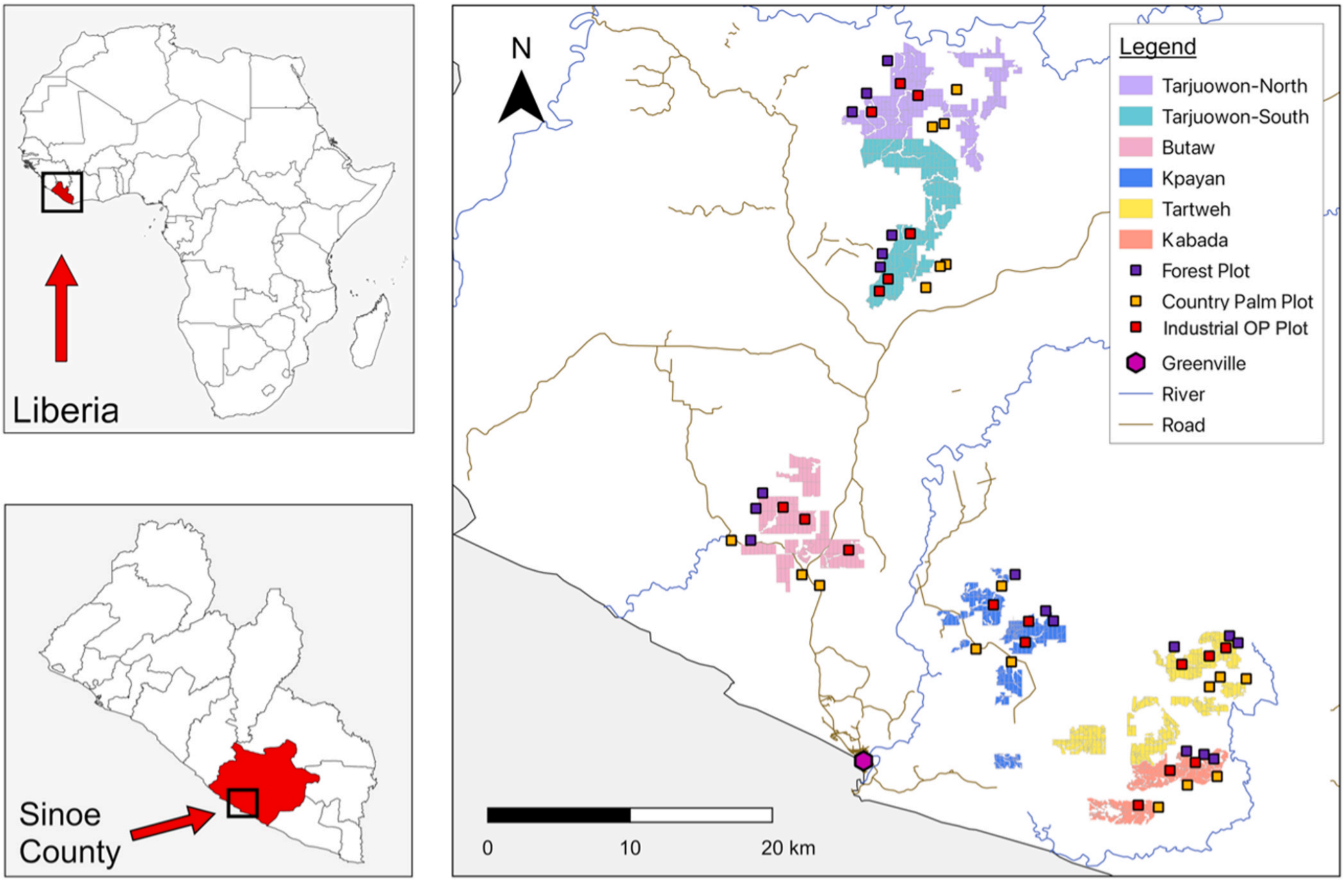

Fig. 1. Map of the SOPWA Project study design in Sinoe County, Liberia. The SOPWA Project features 54 study plots (50 ×50 m; 18 per system). Square colour indicates study system (purple = Forest, orange = Country palm, red = Industrial oil palm ('Industrial OP' in legend)). Plots are clustered around six industrial oil palm farms (owned by Golden Veroleum Liberia), which are shown in blocks of colour. Greenville (pink hexagon), the capital city of Sinoe County, is shown for reference. Blue and brown lines indicate major rivers and roads, respectively. This figure is reproduced from Pashkevich et al. (2024a).

years), and was being restored passively towards secondary forest (called 'low bush' by local communities). When they were actively managed, the farms were small-scale (all were < 5 ha) and local people prepared them using slash-and-burn practices. All farms had natural growing oil palms present, which are fire-resistant and therefore survive the burning. Local people use palm fruits of wild-growing palms to produce cooking oil, and the heart of the palms (the central growing tip) to make palm wine. When these areas were actively farmed, other crops were also grown including cassava, rice, banana, pumpkin, cucumber, pepper, and bitterball (Pashkevich et al., 2024a). The farmers did not apply any chemical fertilisers, pesticides, or herbicides.

2.1.3. *Industrial oil palm*

These plots are in industrial oil palm farms owned and managed by GVL. GVL has six oil palm farms in Sinoe County: Kabada, Tartweh, Kpayan, Butaw, Tarjuowon-South, and Tarjuowon-North (Fig. 1). These farms are certified by the Earthworm Foundation (https://www.earthworm.org) and follow standard management procedures, in line with recommendations provided by Sinar Mas Agro Resources and Technology Research Institute (Kaybee, 2019). At the time of our study, oil palms were aged 5–11 years (Table S3). The farms are monocultures, arranged in 300 x 1000 m blocks, with individual palms planted ~ 8 m apart. Palms are harvested manually on a 10 – 15 day cycle using a chisel or harvesting sickles on telescopic poles, depending on palm height. GVL applies fertilisers and herbicides regularly, and pesticides selectively (when outbreaks of insect pests occur) (Pashkevich et al., 2024a).

SOPWA features 18 plots in each system (N = 54), with plots grouped into six clusters (and each cluster having three plots in each system), based around each of the Sinoe County GVL oil palm farms (Fig. 1). Plots of the same system were > 400 m apart (mean distance between plots was 1.85 km). We established forest and industrial oil palm plots > 200 m from habitat edges, and country palm plots > 200 m from industrial oil palm plantations (a sufficient distance to prevent edge effects from plantations; Lucey and Hill 2012). For full details of study plots and the overall SOPWA design, see Pashkevich et al. (2024a).

2.2. *Data collection*

2.2.1. *Ground-dwelling arthropod sampling*

To assess differences in ground-dwelling arthropod biodiversity across rainforest and oil palm systems, we surveyed ground-dwelling arthropods in all SOPWA plots during January – February 2023 (corresponding to Liberia's dry season). We collected arthropods by setting three pitfall traps in each plot, arranged in a triangular fashion such that each trap was 5 m from the plot centre at bearings 0°, 135°, and 225° (and traps spaced 10 m apart from each other). In total, we deployed 162 traps. Our traps were made from the lower half of disposable plastic water bottles (measuring 6.3 cm in diameter at the mouth, and 11.8 cm deep), and covered with a plastic plate (raised by wooden skewers) to prevent dilution or flooding from rainfall. We filled the traps with a solution of 20 % ethanol and 80 % water, and added three drops of dish soap to break the surface tension. We retrieved the traps after 72 h. During collection, we poured the trap contents into a fine sieve (53 μm mesh), using a spoon and forceps to retrieve any remaining contents within the sieve.

We stored the arthropods in 70 % isopropyl alcohol, and exported the samples to the Museum of Zoology at the University of Cambridge, United Kingdom (export permit number MD/031/2023/-3). Arthropods were identified to order-level using stereomicroscopes, aside from Diplopoda which were identified to class, Formicidae to family, and Isoptera to infraorder due to their unique ecology and easy identification, and to provide complementarity with previous related studies (e.g., Ashton-Butt et al., 2019; Pashkevich et al., 2021). We identified caterpillars as Lepidoptera, since they go through complete metamorphosis and owing to their distinguishable appearance, but we categorised all other larvae to their own group. Hereafter, we refer to all arthropod groups as orders. We identified spiders (important providers of pest control services in oil palm farmlands (Pashkevich et al., 2021)), to morphospecies 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 (2024). Specimens are preserved in the Museum of Zoology, University of Cambridge, and we are in conversations with the Government of Liberia to return a complete morphoseries to Liberia over time.

2.3. *Statistical analyses*

We conducted all statistical analyses using R version 4.3.2 (R Core Team, 2023) within RStudio version 2023.03.1 + 446 (Rstudio team, 2023). We used packages *readxl* (Wickham and Bryan, 2023), *tidyverse* (Wickham et al., 2019), *plyr* (Wickham, 2011), *dplyr* (Wickham et al., 2023), *ggsignif* (Ahlmann-Eltze and Patil, 2021), *vegan* (Oksanen et al., 2022), *BiodiversityR* (Kindt, 2022), and *lemon* (Edwards, 2022) for data wrangling, exploration, and visualisation. We used *glmmTMB* (Brooks et al., 2017) for fitting generalised linear mixed effects models (GLMMs) and *mvabund* (Wang et al., 2022) for fitting multivariate generalised linear models (mGLMs).

Prior to analysis, we pooled pitfall traps from the same plot. During transportation, we lost two pitfall samples. To account for this when pooling samples, we standardised data from these plots by calculating the mean abundance per remaining traps, multiplying by three (the number of traps set), and rounding the value to the nearest integer to meet model assumptions.

2.3.1. *Differences in ground-dwelling arthropod abundance and order-level community composition across systems*

To assess the relative proportion of arthropod orders in each system, we calculated evenness values as the Pielou index (J), which is derived from the Shannon index. The J values range from 1.0 to 0.0, where 1.0 is a community with completely equal relative abundances, and 0.0 is an entirely unequal community. We visualised order-level evenness by plotting rank abundance curves.

We used a GLMM to assess differences in arthropod abundance across forest, country palm, and industrial oil palm systems. We fitted the model to a negative binomial distribution (as the poisson-distributed model was overdispersed) with System (a factor, with levels: forest, country palm, and industrial oil palm) as a fixed effect. We incorporated Farm (levels: Kabada, Tartweh, Kpayan, Butaw, Tarjuowon-South, Tarjuowon-North) as a random intercept effect to account for spatio-temporal dependencies arising from the clustered arrangement of the SOPWA plots and our sampling schedule. Therefore, our model took the form: Abundance $\sim$ System $+ (1|\text{Farm})$. We validated our model by checking for overdispersion and plotting Pearson residuals against fitted values and covariate System to check that no patterns of homoscedasticity or non-linearity were present. We also simulated 10,000 datasets from each model, calculated the dispersion statistics for each dataset, and checked that the dispersion statistic for each model was within the range of the simulation (Zuur and Ieno, 2016). Our validation procedure indicated that there were no problems with our modelling. We determined the significance of System by comparing our GLMMs to null models using likelihood ratio tests (LRTs). Our null models took the form: Abundance $\sim 1 + (1|\text{Farm})$. If System was significant ($P < 0.05$), we conducted pairwise post-hoc tests (Tukey all-pair comparison tests owing to multiple comparisons) to determine which systems differed. Six plots contained > 1000 ants, likely owing to individual traps being in the middle of disturbed ant nests or ant highways during deployment. To test the influence of these samples on our findings, we conducted a sensitivity analysis wherein we removed these plots from our dataset and re-ran our arthropod abundance model.

We used a mGLM to assess differences in order-level community composition of arthropods across forest, country palm, and industrial oil palm systems. Prior to analysis, we removed Neuroptera, Pseudoscorpiones, and Schizomida as they were represented by only a few individuals across the study (total abundance across all sites < 5 for all) and caused model convergence issues. We fitted our model to a negative binomial distribution (due to a poisson-distributed model being overdispersed) with System as a fixed effect. We used Farm as a blocking variable to account for non-independence of plots within the same cluster. Our model therefore took the form: Arthropod order-level community composition $\sim$ System $+ (1|\text{Farm})$. We validated our mGLM by plotting Dunn-Smyth residuals against fitted values and covariate System and ensuring no relationships were present. We determined the effect of System on arthropod order-level community composition using a LRT and by bootstrapping probability integral transform (PIT) residuals with 10,000 resampling iterations (Warton et al., 2017). If System was significant ($P < 0.05$), we ran univariate analyses to determine which orders differed significantly in abundance across the three study systems, therefore driving changes in community composition. We used a step-down resampling algorithm to adjust univariate P-values for multiple testing (Wang et al., 2012). We visualised our order-level arthropod community composition findings using stacked bar charts, and an ordination plotted from the posterior medians of a Bayesian generalised linear latent variable model (GLLVM) using the *boral* package (Hui, 2021). We fitted a pure (i.e., no covariates included) GLLVM but fitted Farm as a random row effect to account for spatiotemporal dependences in our dataset, as described above. As with our mGLM, we removed Neuroptera, Pseudoscorpiones, and Schizomida from the dataset before fitting our GLLVM.

2.3.2. Differences in ground-dwelling spider abundance, species richness and species-level community composition across systems

To assess our sampling completeness, we calculated interpolated and extrapolated species accumulation curves for adult spiders only in each system (package *iNEXT*; Hsieh et al., 2022). We extrapolated to double the number of individuals found in each system.

We assessed differences in total spider abundance (including adults and juveniles) and species richness (adults only) using poisson-distributed GLMMs. We fitted and validated our models as described for all arthropods above. When analysing differences in spider species richness, our model validation procedure indicated that model assumptions were not being met, and therefore we re-analysed these data with a Kruskal-Wallis test using *stats* (R Core Team, 2023), and

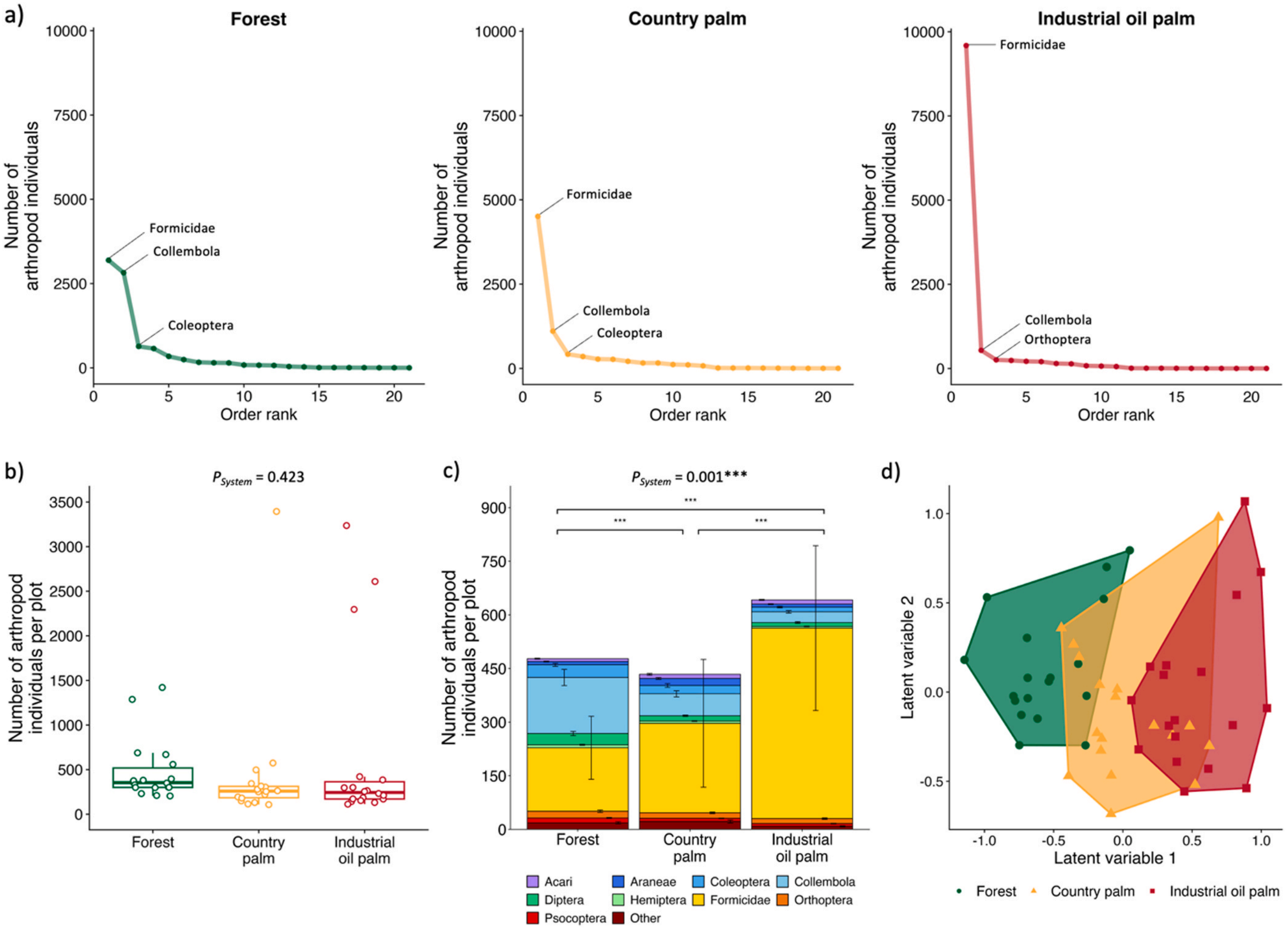

Fig. 2. Differences in order rank abundance (a), total abundance (b), and order-level community composition (c-d) of arthropods across forest, country palm, and industrial oil palm systems. For (b) and (c), the effect of System on each response (determined using LRTs) is shown above in text, and when this was significant ($P < 0.05$), results of pairwise post-hoc analyses are indicated by the horizontal lines above each plot: * **$P < 0.001$, * *$P < 0.01$, *$P < 0.05$. For (b), boxplots show median (horizontal crossbar) and interquartile ranges, and the circular datapoints show the per-plot values. In (c), the nine most abundant arthropod orders across all samples are plotted in order of the legend and error bars show the standard error of the mean. (d) visualises the differences in arthropod order-level community composition in multi-dimensional space. Points indicate the posterior medians of the GLLVM and, to help visualisation, we drew hulls around points of the same system.

conducted post-hoc analyses using the Dunn's Test for multiple comparisons (package *dunn.test*; Dinno, 2017), adjusting our P-values using the Bonferroni correction. We assessed differences in spider species-level composition (adults only) using a poisson-distributed mGLM and GLLVM. Otherwise, our mGLM and GLLVM were fitted and validated, and findings visualised, as described above.

3. Results

3.1. *Differences in ground-dwelling arthropod abundance and order-level community composition across systems*

We collected 28,077 arthropods representing 21 orders. This included 8661 arthropods in forest, 7844 arthropods in country palm, and 11,572 arthropods in industrial oil palm. Formicidae ($n = 3194$), Collembola ($n = 2820$), and Coleoptera ($n = 636$) were dominant in forest; Formicidae ($n = 4508$), Collembola ($n = 1105$), and Coleoptera ($n = 420$) were dominant in country palm; and Formicidae ($n = 9590$), Collembola ($n = 539$), and Orthoptera ($n = 255$) were dominant in industrial oil palm (Fig. 2a). Pielou indices indicated that order evenness was higher in forest ($J = 0.590$) and country palm ($J = 0.524$) than in industrial oil palm (0.288) (Fig. 2a).

We found no significant differences in per-plot arthropod abundance across forest (mean ($\bar{x}$) per plot ± standard error (SE) = 481 ± 82), country palm ($\bar{x}$ ± SE = 438 ± 176), and industrial oil palm ($\bar{x}$ ± SE = 643 ± 229) systems (LRT = 1.720, $P = 0.423$; Fig. 2b; all model summaries in Tables S1 and S2). Our sensitivity analysis, wherein we removed plots with > 1000 ants, indicated significant differences in arthropod abundance across our study systems (LRT = 11.59, $P = 0.003$; Fig. S2). Post-hoc analyses indicated that arthropod abundance in forest ($\bar{x}$ ± SE = 372 ± 36.6) was over 1.4 and 1.6 times higher than in country palm ($\bar{x}$ ± SE = 262 ± 30.5) and industrial oil palm ($\bar{x}$ ± SE = 229 ± 23.7), respectively (post-hoc comparisons: forest – country palm: $P = 0.029$; forest – industrial oil palm: 0.002). We found no significant differences in arthropod abundance between country palm and industrial oil palm ($P > 0.05$).

Arthropod order-level community composition differed significantly across systems (LRT = 202.4, $P < 0.001$; Fig. 2c-d). Post-hoc analyses showed significant differences between all systems ($P \leq 0.001$ for all). Univariate analyses indicated that compositional changes were driven by differences in the relative abundance of Araneae ($P = 0.025$), Collembola ($P < 0.001$), Dermaptera ($P = 0.024$), and Diptera ($P = 0.046$) (Fig. 2c). Mean Araneae abundance was highest in country palm ($\bar{x}$ ± SE = 19.6 ± 2.49); it was over 2.1 and 2.4 times higher, respectively,

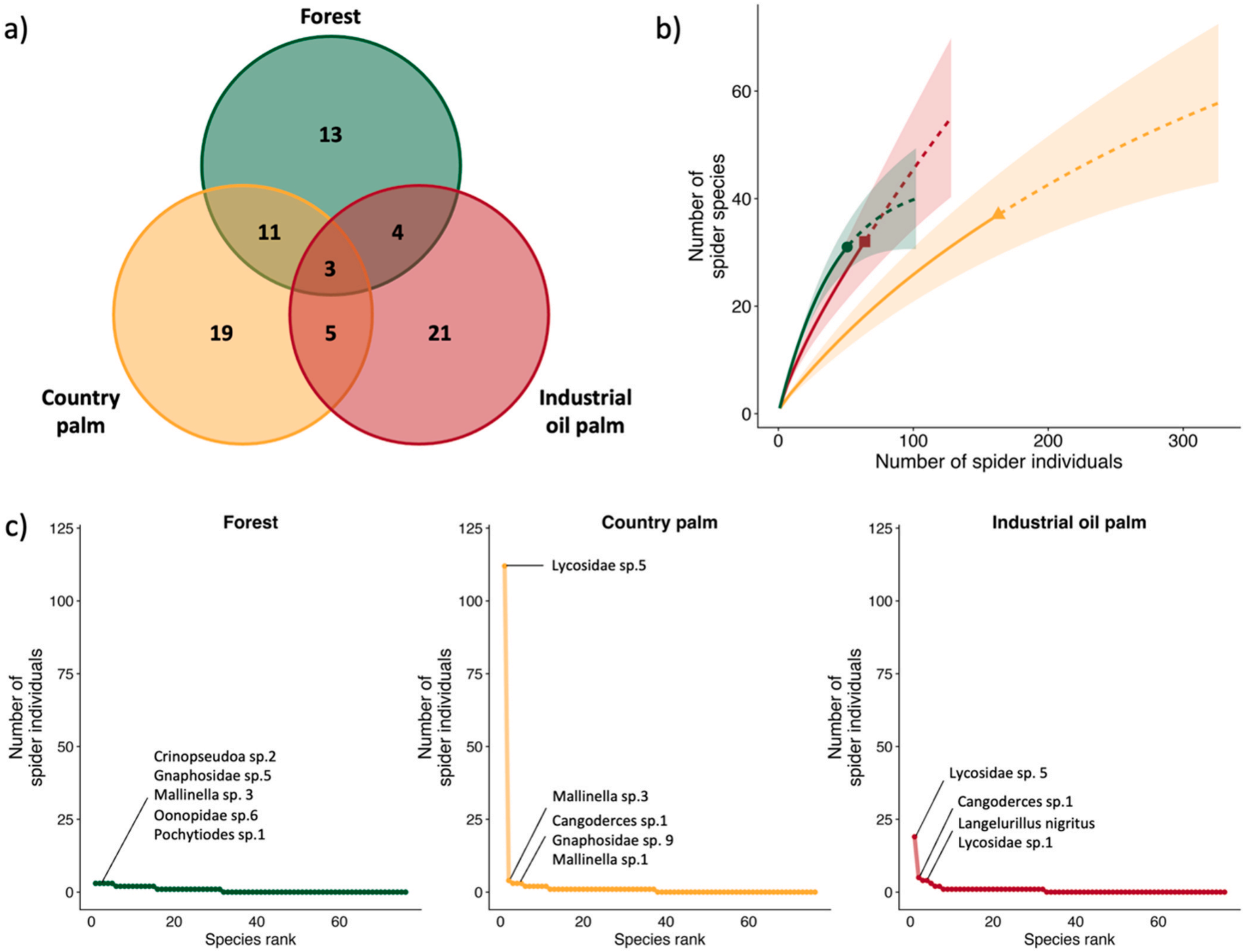

Fig. 3. The number of species (a), and species accumulation curves (b), and species rank abundance curves (c) of ground-dwelling spiders found in forest, country palm, and industrial oil palm systems. We note that only adult spiders were considered in these analyses, as the juvenile spiders were not identified to morphospecies-level. For (a), numbers indicate the total number of spider species found in each system and the number of species shared between systems. For (b), we plotted both interpolated (solid line) and extrapolated (dashed line) curves. For (c), we included the names of the most abundant species in each system, and axes are consistent across subplots to facilitate comparisons across systems. We extrapolated to double the number of individuals found in each system.

than in forest ($\bar{x} \pm SE = 9.11 \pm 1.35$) and industrial oil palm ($\bar{x} \pm SE = 8.17 \pm 1.38$) (Fig. S2). Mean Collembola abundance in forest ($\bar{x} \pm SE = 157 \pm 22.8$) was over 2.5 and 5.2 times greater than country palm ($\bar{x} \pm SE = 61.4 \pm 8.60$) and industrial oil palm ($\bar{x} \pm SE = 29.9 \pm 3.52$), respectively. Mean Dermaptera abundance in country palm ($\bar{x} \pm SE = 5.78 \pm 3.15$) was over 1.4 and 5.7 times higher than forest ($\bar{x} \pm SE = 4.00 \pm 1.73$) and industrial oil palm ($\bar{x} \pm SE = 0.00 \pm 0.00$), respectively, whilst mean Diptera abundance in forest ($\bar{x} \pm SE = 31.8 \pm 5.88$) was over 2.1 and 2.8 times greater than country palm ($\bar{x} \pm SE = 14.9 \pm 1.97$) and industrial oil palm ($\bar{x} \pm SE = 11.2 \pm 2.28$), respectively (Fig. S2).

3.2. Differences in ground-dwelling spider abundance, species richness and species-level community composition across systems

We collected 663 spiders representing 76 species. This included 164 spiders in forest ($n_{adults} = 54$, $n_{species} = 31$), 352 spiders in country palm ($n_{adults} = 163$, $n_{species} = 38$), and 147 spiders in industrial oil palm ($n_{adults} = 65$, $n_{species} = 33$) (Fig. 3a). Species accumulation curves were still increasing in all systems, indicating an imperfect sampling completeness, particularly in industrial oil palm (Fig. 3b). Five species from five families accounted for 28 % of spiders in forest (Crinopseudoa sp.2, Gnaphosidae sp.5, Mallinella sp.3, Oonopidae sp.6, Pochytoides sp.1; n = 3 for all). A singular species of Lycosidae (Lycosidae sp.5, n = 112) accounted for 69 % of spiders in country palm. Four species

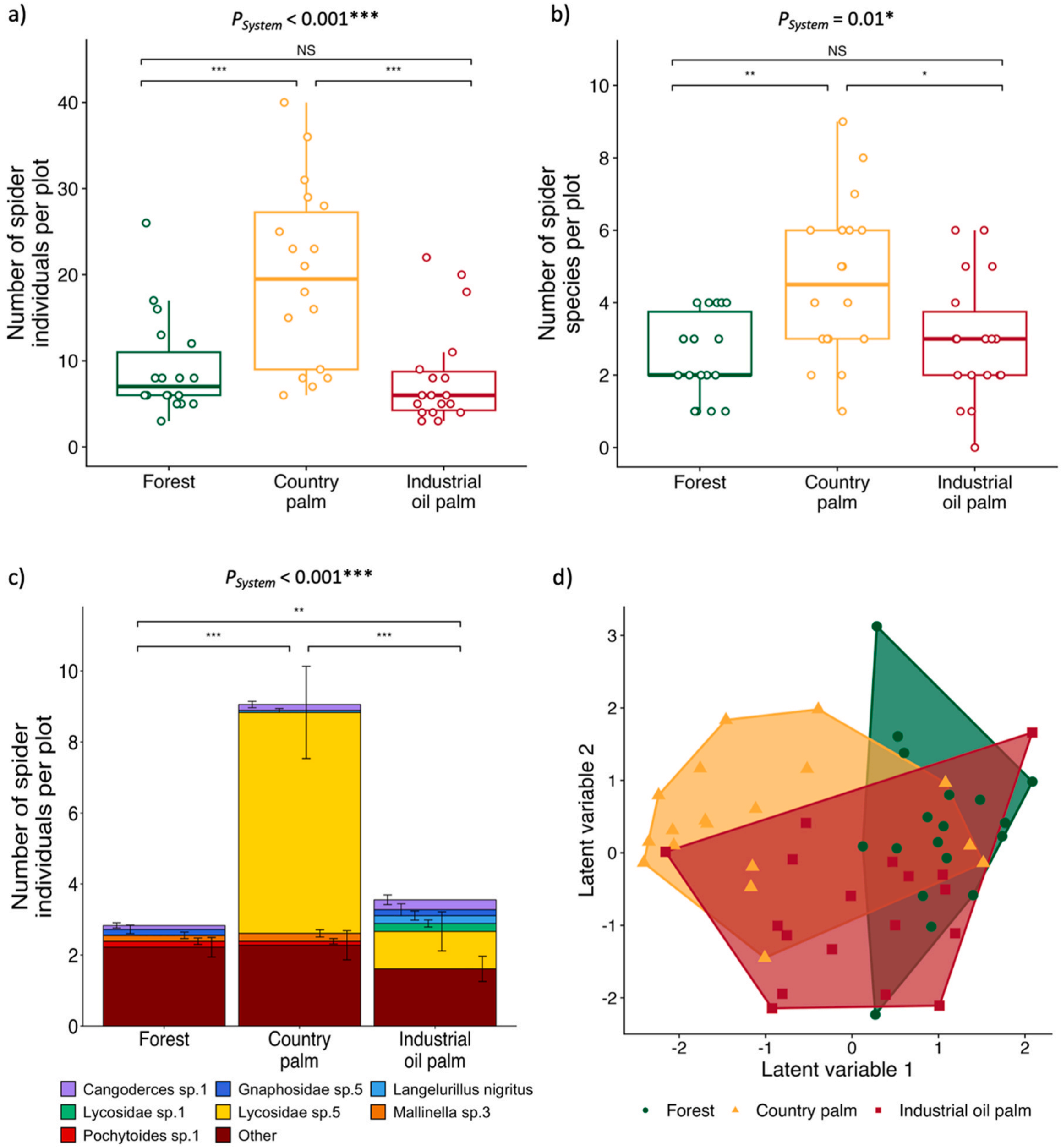

Fig. 4. Differences in total spider abundance (a), species richness (b), and species-level community composition (c-d) across forest, country palm, and industrial oil palm systems. For plots (a-c), the effect of System on each response (determined using LRTs) is shown above in text, and results of pairwise post-hoc analyses are indicated by the horizontal lines above each plot: * **P < 0.001, * *P < 0.01, *P < 0.05. For (a) and (b), boxplots show median (horizontal crossbar) and interquartile ranges, and the circular datapoints show the per-plot values. In (c), the seven most abundant spider species in each system are plotted in order of the legend and error bars show the standard error of the mean. Plot (d) visualises the differences in spider species-level community composition. Points indicate the posterior medians of the GLLVM, and to help visualisation we drew hulls around points of the same system.

from three families accounted for 49 % of spiders in industrial oil palm (Lycosidae sp. 5, n = 19; Cangoderces sp. 1, n = 5; *Langelurillus nigritus*, n = 4; Lycosidae sp.1; n = 4) (Fig. 3c). Pielou indices indicated that species evenness was highest in forest ($J = 0.971$) and industrial oil palm ($J = 0.834$), and lowest in country palm (0.472) (Fig. 3c).

We found significant differences in spider abundance across forest, country palm, and industrial oil palm systems (LRT = 20.18, $P < 0.001$; Fig. 4a). Post-hoc analyses indicated that spider abundance in country palm ($\bar{x} \pm SE = 19.6 \pm 2.49$) was over 2.1 and 2.3 times higher than in forest ($\bar{x} \pm SE = 9.11 \pm 1.35$) and industrial oil palm ($\bar{x} \pm SE = 8.17 \pm 1.38$), respectively ($P < 0.001$ for both). We found no significant differences in spider abundance between forest and industrial oil palm ($P > 0.05$).

Spider species richness differed significantly across forest, country palm, and industrial oil palm systems ($x^2 = 9.958$, $P = 0.01$; Fig. 4b). Mean spider species richness in country palm ($\bar{x} \pm SE = 4.61 \pm 0.519$) was over 1.8 and 1.5 times higher than in forest ($\bar{x} \pm SE = 2.50 \pm 0.271$) and industrial oil palm ($\bar{x} \pm SE = 2.94 \pm 0.400$), respectively (post-hoc comparisons: forest – country palm: $P = 0.004$; forest – industrial oil palm: $P = 0.726$; country palm – industrial oil palm: $P = 0.031$).

Spider species-level community composition differed significantly across forest, country palm, and industrial oil palm systems (LRT = 390.4, $P < 0.001$; Fig. 3c-d). Post-hoc analyses showed significant differences between all systems (forest – country palm: $P < 0.001$; forest – industrial oil palm: $P = 0.001$; country palm – industrial oil palm: $P < 0.001$). Univariate analyses indicated that compositional differences were driven primarily by changes in the relative abundance of Lycosidae sp.5 ($P < 0.001$) (Fig. 3c). Mean Lycosidae sp.5 abundance in country palm ($\bar{x} \pm SE = 6.22 \pm 1.30$) was over 6.2 and 5.8 times higher than in forest ($\bar{x} \pm SE = 0.00 \pm 0.00$) and industrial oil palm ($\bar{x} \pm SE = 1.06 \pm 0.551$), respectively.

4. Discussion

In this study, we investigated differences in the biodiversity of ground-dwelling arthropods across forest, country palm, and industrial oil palm systems in Sinoe County, Liberia. Across our study systems, we found no differences in total arthropod abundance, although we did find significant differences in arthropod order-level community composition, and spider abundance, species richness, and species-level community composition.

4.1. Impacts of traditional and industrial approaches to oil palm cultivation on ground-dwelling arthropods

Arthropod abundance did not differ significantly across forest, country palm, and industrial oil palm systems. This is somewhat surprising, as rainforest conversion to country palm and industrial oil palm, and subsequent on-farm management, causes considerable changes in vegetation complexity, diversity, and microclimate (Pashkevich et al., 2024a). In country palm, practices include burning smaller areas of rainforest to plant annual crops for subsistence, and allowing vegetation to grow back in the surrounding areas after one to two years. In industrial oil palm, practices include the conversion of large areas of rainforest to oil palm monocultures, and regular application of inorganic fertilisers and herbicides. Previous work has shown that arthropods are sensitive to environmental changes resulting from farm establishment and management (Mumme et al., 2015; Turner and Foster, 2009). For instance, a study in Indonesia found that conversion of rainforest to oil palm plantations reduced the species richness and density of litter-dwelling invertebrates by 46 % and 48 %, respectively (Mumme et al., 2015). Overall, our arthropod abundance findings are encouraging for conservation as they indicate that the total number of ground-dwelling arthropods is not reduced when converting native rainforest to oil palm systems in Liberia. However, our sensitivity analysis demonstrated that the lack of difference in arthropod abundance was conditional on including samples that had a high abundance of ants, owing to the presence of ant nests or highways in the vicinity of traps. When these traps were excluded from our analysis, we found that total arthropod abundance was highest in the forest plots. This indicates that ants may contribute a greater proportion of the total number of arthropods in country palm and industrial oil palm systems than in forest, and that the species that were in the highways/nests (and therefore had substantial influence on our initial model's findings) were generalists that thrive in high-disturbance farming systems. This is supported by previous work in oil palm plantations, for instance, Hood et al. (2020) found that seven generalist species comprised 78 % of ant individuals in oil palm, despite finding 68 species across their study sites. While these outliers are real datapoints, they may suggest that arthropod abundance in oil palm systems is more variable than in forest, which may result in greater vulnerability to environmental stressors, such as climate change, over the long-term.

Although there were no differences in total arthropod abundance across our study systems, we did find significant differences in the abundance of individual orders, therefore causing changes in arthropod community composition. In particular, we found differences in the abundance of Araneae, Collembola, Dermaptera, and Diptera. Our order-level findings were further magnified in our spider-specific analyses, which showed that oil palm cultivation influences spider abundance, species richness, and species-level community composition. Collectively, these findings indicate that traditional and industrial approaches to oil palm cultivation influence arthropod biodiversity, owing to group- and species-specific sensitivities to land use changes and management. We note that some arthropod orders and spider species benefitted from oil palm cultivation, whilst others did not, indicating that there are "winning" and "losing" species as rainforest is converted to oil palm systems. In particular, our findings indicate that Collembola and Diptera "lose" as forest is converted to oil palm, likely owing to the high sensitivity of Collembola and Diptera to changes in microclimatic conditions, litter mass, soil structure and pH, all of which occur as a result of oil palm cultivation practices (Mumme et al., 2015; Pramual and Kuvangkadilok, 2009; Sousa et al., 2006; Susanti et al., 2021). Indeed, Susanti et al. (2021) demonstrated that changes in soil water content and pH drove declines in the biodiversity of litter dwelling Collembola as rainforests were converted to oil palm plantations in Indonesia. On the other hand, country palm supported substantially higher Araneae and Dermaptera abundances than forest and industrial oil palm. Although we did not test the response of arthropods to environmental variables in this study, the high abundance of ground-dwelling Araneae and Dermaptera could be attributed to three possible effects. Firstly, country palm has intermediate levels of human activity, relative to industrial oil palm (higher human activity, owing to harvesting and management) and rainforest (lower human activity), which may allow both forest-dependant and generalist species to inhabit these systems (Bruggisser et al., 2010; Tajthi et al., 2017; Tsai et al., 2006; Zheng et al., 2017). Secondly, in comparison to industrial oil palm, country palm is less intensely managed; no chemical fertilisers, pesticides, or herbicides are applied to boost crop growth, allowing thick vegetation (called 'low bush' by local people) to develop. This dense and complex understory and midstory vegetation provides a wide variety of microhabitats, more similar to rainforest (Pashkevich et al., 2024a), for different ground-dwelling species to hunt, reproduce, and take shelter in. Thirdly, the lack of on-farm management and thick understory vegetation in country palm may support more insects, plants (Marshall et al., 2024), and decaying matter on which Araneae and Dermaptera feed, increasing their resource availability and allowing their populations to flourish. This result is similar to other studies which have found that agricultural plantations with higher levels of understory vegetation (similar to country palm) support relatively more biodiverse spider communities (Pashkevich et al., 2021, 2022; Potapov et al., 2020). For instance, a study in Indonesia found that jungle rubber plantations (disturbed rainforest habitats planted with rubber trees) supported ground-dwelling spider communities that were more diverse and had greater biomass compared with oil palm monocultures (Potapov et al., 2020). However, it is noteworthy that a previous study in the SOPWA Project area found that country palm supported fewer web-building spiders in the understory, relative to rainforest and industrial oil palm, likely because vegetation density in this system was so high that it limited space for spider web-building (Pashkevich et al., 2024b). In comparison, most of the spiders in our current study were not web-builders but rather active hunters or stalkers that run on the ground. Collectively, the findings of this study and Pashkevich et al. (2024b) indicate the importance of studying multiple microhabitats when assessing how land use changes and management influence biodiversity, even within a single taxonomic group. We note a few factors which may have influenced our arthropod order-level and spider species-level results. Firstly, the SOPWA study region has distinct wet and dry seasons, and we surveyed during the dry season only. It is possible that seasonal conditions, such as lower levels of cloud cover in comparison to the rainy season, could have amplified differences in microclimate and, as a result, arthropod biodiversity between systems (Pashkevich et al., 2024a). Second, our spider species accumulation curves were still increasing, particularly in industrial oil palm, and therefore spider biodiversity in each system may be higher than this study indicates. The extrapolated curves suggested that, despite having the highest alpha spider diversity (species richness per plot), country palm did not have the highest total number of species across all systems. Country palm is a system in flux; our plots were in abandoned farms that were being passively restored to secondary forest. Our findings may suggest that country palm supports abundant populations of both generalist and specialist spider species, but species turnover is high. Third, our spider abundance and species-level composition findings were driven primarily by a single species of Lycosidae in country palm, which was highly abundant in this system. Fourth, previous work has shown that arthropod biodiversity in industrial oil palm plantations changes over time (Pashkevich et al., 2021), likely owing to microclimatic changes that occur as oil palm canopies close with age. Our industrial oil palm sites had palms aged between 5 and 11 years (Table S3). While oil palms in all sites were fruiting (i.e., were sexually mature), canopies had not completely closed in the younger sites, and it is possible that levels of arthropod biodiversity in industrial oil palm will become more similar to those in rainforest and country palm over time.

Differences in Araneae, Collembola, Dermaptera, and Diptera abundance could affect levels of ecosystem functioning across systems. Araneae are natural predators of many insect species, including oil palm pests such as slug moth caterpillars (family: Limacodidae; *Parasa* spp.) and bag worms (family: Psychidae) that damage crop yields, but also pollinators such as the African oil palm weevil (*Elaeidobius kamerunicus*) that are vital for crop growth (Corley and Tinker, 2016; El-Nabawy et al., 2016; Michalko et al., 2019). Maintaining high abundances of Araneae within industrial oil palm plantations may lead to increased predation of pests, and potentially higher crop yields. Collembola and Dermaptera play a key role in decomposition and are prey for other arthropods, whilst Diptera are pollinators and decomposers (Coulibaly et al., 2019; Happe et al., 2018; Kocárek et al., 2005; Mawan et al., 2022; Skevington and Dang, 2002). Therefore, the differences in arthropod biodiversity that we found across forest, country palm, and industrial palm systems are not only important for conservation but also oil palm yields, owing to the vital ecosystem functions that many arthropod species provide.

5. Management implications and conclusions

To our knowledge, this is the first study to evaluate the impacts of traditional and industrial oil palm cultivation on ground-dwelling arthropods in Liberian rainforest landscapes, building on our knowledge of environmental conditions (Pashkevich et al., 2024a), understory spiders (Pashkevich et al., 2024b) and plants (Marshall et al., 2024). Despite their essential roles in ecosystems, very little research has been conducted on arthropods in West Africa and especially in Liberia (Kass et al., 2022; Miller and Rogo, 2001; van Klink et al., 2020). For example, in a global meta-analysis focused on long-term trends in insect populations over time (van Klink et al., 2020), datasets from West Africa were almost entirely absent. Our study therefore provides important baseline ecological data in an understudied region, indicating clearly that rainforest and agricultural systems support different arthropod communities and highlighting the critical importance of conserving rainforest habitats in this region. Our study is also one of the first to assess, and quantify the ecological value of, Liberian country palm systems, which are one form of traditional local approaches to cultivating oil palm in West Africa. Country palm is highly important to communities in the region, as palm oil is a staple food and economically beneficial for farmers who sell it at local markets. Our results showed that country palm often supports ecological communities that are between those found in forest and industrial oil palm systems. Although we found that country palm supported different arthropod communities to forest, arthropod order-level community composition in country palm and forest was considerably more similar than that in forest and industrial oil palm. Our results therefore suggest that country palm has unique ecological value. However, from an oil palm production perspective, the industrial oil palm plantations are likely to have far higher yields (owing to application of fertilisers and planted high-yielding varieties), leading to trade-offs between biodiversity conservation and crop production over time. We recommend further research which quantifies the differences in yield between country palm and industrial oil palm systems in Liberia, to better understand yield-conservation trade-offs.

Importantly, our findings indicate that traditional and industrial oil palm cultivation systems can still support relatively biodiverse and abundant ground-dwelling arthropod communities. Efforts should be made within these systems to minimise negative impacts of oil palm cultivation on native arthropod assemblages, and to conserve arthropod biodiversity and enhance beneficial ecosystem services (e.g., pollination and pest control) that many species provide. While research in Southeast Asia has investigated the impacts of management practices on arthropods in oil palm systems, such studies are relatively rare in West Africa (Pashkevich et al., 2024a). We therefore review these practices here in light of our findings, and discuss how they are or could be implemented in Liberian oil palm plantations. We note that we have not tested these management methods in this study, and therefore the potential impacts of the following management methods in West Africa may differ from those observed in Southeast Asia. Firstly, conserving forest fragments within or near plantations can be beneficial for both arthropod biodiversity and oil palm yields, owing to some spillover of pollinating and predatory arthropods (Lucey et al., 2014; Lucey and Hill, 2012). For instance, a study in Malaysia found that large forest fragments around oil palm plantations increased carnivorous ant biodiversity in the surrounding area, potentially assisting within-plantation pest control (Lucey et al., 2014). Secondly, promoting growth of understory vegetation by reducing herbicide application within plantations has been shown to benefit arthropod biodiversity (Ashton-Butt et al., 2018), by allowing for higher vegetation diversity and coverage and therefore supporting more microhabitats within plantations (Luke, et al., 2019a). Ashton-Butt et al. (2018) studied the impact of different understory vegetation treatments and found that soil macrofauna abundance and order richness was higher in plots with enhanced understory vegetation. Thirdly, growing oil palm as a polyculture and establishing diverse tree islands has also been shown to benefit arthropod biodiversity in oil palm, owing to increases in vegetation complexity and diversity (Ashraf et al., 2018; Ghazali et al., 2016; Nasi, 2023; Zemp et al., 2023). For example, a study in Malaysia found that arthropod abundance and order- and family-level richness were significantly greater in alley-cropping oil palm farms compared with oil palm monocultures (Ghazali et al., 2016), whilst a study in Indonesia found that diverse tree islands in oil palm landscapes increase the species richness and diversity of arthropods and soil fauna within plantations (Zemp et al., 2023). When considering whether to implement any of these strategies, trade-offs between arthropod conservation and palm oil yields must be considered, with the most desirable strategies being those that enhance biodiversity and benefit – or have no effect on - crop production. Aside from maintaining forest fragments, there was limited uptake of any of these strategies in the industrial oil palm plantations in which we sampled. The West African oil palm industry should be supported in testing and – only if they are found to successfully enhance biodiversity, ecosystem service delivery, and crop yields – incorporating strategies, such as those described above, into their farm management plans moving forward. Identifying such strategies is a key component to ensuring the long-term sustainability of the West African oil palm industry.

CRediT authorship contribution statement

Jonathan H. Timperley: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michael D. Pashkevich:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Edgar C. Turner:** Writing – review & editing, Supervision, Conceptualization. **Brogan L. Pett:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Benedictus Freeman:** Writing – review & editing, Conceptualization. **Ari Saputra:** Data curation, Conceptualization. **Cicely A.M. Marshall:** Writing – review & editing. **Bility Geninyan:** Data curation. **Romeo Weah:** Data curation. **Abraham Vincent:** Data curation. **Rudy H. Widodo:** Conceptualization. **Morris T. Jah:** Data curation. **Tiecanna Jones:** Data curation. **Marshall Guahn:** Data curation. **Peter M. Hadfield:** Conceptualization.

Author contributions

JHT led data collection (with assistance from **BG, AS, AV, RW**, and **MDP**), statistical analyses, and writing of the manuscript. **BP** identified the spiders. **AS, BF, MG, PMH, MTJ, TJ, RHW, CAMM, ECT**, and **MDP** helped to design and facilitate the larger administration of the SOPWA Project, in which this study was based. All authors approved the manuscript.

Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109626.

Data availability

All data associated with this article can be found in Apollo: the data repository of the University of Cambridge.

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