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RESEARCH ARTICLE

# Plant biodiversity, vegetation structure and provisioning services in rainforest, traditional and industrial oil palm cultivation systems in Liberia, West Africa

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**Societal Impact Statement**

Oil palm is native to the west African forest, where industrial production is expanding. We assessed differences in plant biodiversity, vegetation structure and provisioning services across 54 forest, community agriculture and oil palm plots in Sinoe County, Liberia. Traditional cultivation systems have lower ecological impacts in terms of species richness, composition, canopy height and structural complexity compared with industrial production, though yields per hectare are likely to be lower. Traditional systems can inspire improved management of industrial plantations, including choice of cover crop, intercropping with locally valued species and reduced clearance and pesticide regimes, increasing biodiversity and local food security.

**Summary**

- Tropical agriculture contributes to national and global food security, but the conversion of natural habitats to agriculture has severe consequences for biodiversity, ecosystem functioning and society. Significant research efforts have focussed on improving the sustainability of palm oil production in Asia, but less research has been conducted in the African forest zone, where oil palm is native and production is expanding.
- Working within the Sustainable Oil Palm in West Africa (SOPWA) Project (Sinoe County, Liberia), we surveyed canopy trees and understorey plants in 54 plots distributed equally across three ecological systems - rainforest, traditionally-cultivated oil palm ("country palm") and industrially-managed oil palm - to assess differences in plant biodiversity, vegetation structure and provisioning services.
- Traditionally-cultivated oil palm systems had intermediate plant biodiversity (species richness, weighted endemism) and structure (canopy height, complexity) compared with industrial production or rainforest. Provisioning services (proportion of species supplying non-timber forest products) did not differ by the system on

average, though the absolute number of useful species recorded was highest for the forest. Of surveyed plant species, 81% had a local name (Sapo or Kru); a smaller proportion of forest species were named compared with either traditional or industrial oil palm systems.

- Our study emphasises the higher ecological value per hectare of traditional oil palm production compared with industrial production methods, though yields are likely to be lower, leading to implications for industrial management such as growing alternative cover crop species, intercropping with non-timber forest products or locally valued crops and implementing reduced clearance and pesticide regimes.

**KEYWORDS**

*Elaeis guineensis*, ethnobotany, land use change, rain forest, traditional agriculture, tropical agriculture

## 1 | INTRODUCTION

Tropical agriculture is critical to food security, human health and livelihoods, but conversion of natural habitat for agriculture has led to substantial losses in biodiversity and related ecosystem functions and services, such as declines in above- and below-ground carbon stocks, wild food supply and changes to traditional livelihoods and culture (Drescher et al., 2016; Li, 2018; Pye, 2019; Santika et al., 2021; Yuliani et al., 2020). Oil palm (*E. guineensis*) is a cash crop grown extensively across the tropics to produce palm oil, the most traded vegetable oil worldwide (USDA, 2024). Its popularity owes partly to its high productivity and profitability, 2.5–6 times more oil is produced per unit area than soybean and oilseed rape, the next most produced vegetable oils, and around twice that of coconut, a comparable tropical forest oil crop (Meijaard et al., 2020). Oil palm plantations are found in at least 49 countries with a combined area of 19.60 Mha (Descals et al., 2021). Expansion of these plantations has driven declines in biodiversity (Barnes et al., 2014), ecosystem functioning (Dislich et al., 2017) and increasing greenhouse gas emissions (Drewer et al., 2021). As much as 27% of global forest loss from 2001 to 2015 can be attributed to commodity-driven deforestation, with permanent land use change to agriculture (including oil palm), mining or energy infrastructure (Curtis et al., 2018). Ecosystems such as savanna and peatlands are also affected by conversion (Fleiss et al., 2022; Warren-Thomas et al., 2022).

Significant research effort has assessed and aimed to mitigate the environmental impacts of palm oil production in Asia (Drescher et al., 2016; Ewers et al., 2011; Luke et al., 2020), where about 80% of the palm oil traded globally is produced, but relatively little research has so far been conducted in the African forest zone (Pashkevich et al., 2024), where oil palm is native and production is expanding in many regions (Davis et al., 2020; Descals et al., 2021). Oil palm has been grown commercially in Africa since at least the eighteenth century, using industrial plantation-style methods since 1909 (Corley & Tinker, 2016). As in SE Asia, oil palm in Africa is cultivated by large-scale industries and individual smallholders in monoculture settings, but unlike in SE Asia, it is additionally harvested from wild-growing palms and has been harvested by local people for thousands of years (Kay et al., 2019). Recent increases in African oil palm cultivation have been driven by both large-scale corporations (e.g. in southeast Liberia, Davis et al., 2020), and smallholders (e.g. in southwest Cameroon, Ordway et al., 2017).

Liberia's two civil wars (1989–1997, 1999–2003), and a historically low population density, contributed to Liberia retaining the highest density of rainforest in west Africa, which as a consequence of the wars are also some of the least studied rainforest areas of Africa and thus globally (Malhi et al., 2013). Nearly one-fifth of its forested area has been lost to agricultural, logging and mining activities, especially since 2003, when the Government of Liberia began promoting large-scale land development for economic recovery (Davis et al., 2020). In Sinoe County Liberia, a county heavily influenced by the oil palm industry, most industrial plantations have been established by Golden Veroleum Liberia (GVL), a member of the Singapore-based Golden Agri-Resources (GAR) group. In Sinoe County, GVL is currently cultivating oil palm on c. 13,000 ha, with c. 11,500 ha set-aside as High Conservation Value areas (HCV, sensu the Roundtable on Sustainable Palm Oil). GVL established its first oil palm farms in Sinoe County in 2012 and currently has six oil palm farms in the County. Liberian people have traditionally relied on shifting cultivation for their livelihoods, burning small areas of rainforest (c. 1 ha) annually for the cultivation of crops including rice, cassava, yams, banana and bitterball (*Solanum*). When preparing lands for farming, areas with wild-growing oil palms (called 'country palms' by local communities) are selected, which grow in low-lying somewhat swampy ground and therefore survive the burning process whilst other trees are felled (Sowunmi, 1999). The density of palms maintained is low enough to allow other crops to receive sunlight, even if the country palms are fully grown (Pashkevich et al., 2024). While harvesting from these wild-growing palms, people also collect other non-timber forest products (NTFP) from wild-growing plant species growing amongst their crops or within fallowed areas. Though most palm oil produced worldwide is interesterified (a food manufacturing process used to change melting point and plasticity), deodorised and decolourised before entering global food, cosmetic or biofuel processing systems, in Liberia palm oil has long been and remains a substantial part of the diet, consumed in soups and stews following light domestic processing of the raw fruit to extract a flavoursome red oil. Sap from the palm is also collected for fermenting and consumption as palm wine. Oil palm cultivation in Liberia is thus integral to peoples' livelihoods, history and culture, in addition to being a profit-making activity.

Industrial oil palm cultivation is expected to have different impacts in Africa compared to industrial production in other well-studied regions due to differences in climate, culture, ecology and management, whilst traditional approaches to oil palm cultivation, about which very little information is so far available, are also expected to differ substantially from industrial production methods developed in Asia (Pashkevich et al., 2024). Here, we assess differences in the biodiversity (species richness, composition, weighted endemism), vegetation structure (canopy height, structural complexity) and provisioning services (proportion of wild plant species supplying non-timber forest products, proportion of named plant species) of plants in the understorey and canopy of rainforest and two styles of oil palm cultivation - traditionally-managed agriculture with wild-growing oil palms, 'country palm' and industrial oil palm plantations - in Sinoe County, Liberia. Our study establishes botanic, ethnobotanic and forest structural baselines within a large-scale research programme – the Sustainable Oil Palm in West Africa (SOPWA) Project – that is evaluating the relative socioecological impacts of oil palm cultivation under traditional and industrial management in Liberia.

# 2 | MATERIALS AND METHODS

## 2.1 | Study site and plot design

We carried out fieldwork in Sinoe County, Liberia (5.135195 N, 9.078423 W) as part of the Sustainable Oil Palm in West Africa (SOPWA) Project (Pashkevich et al., 2024). The mean annual temperature in the region is 25.7°C; mean annual rainfall is 2507.3 mm falling in two distinct wet seasons (April – June, September–October) (calculated over 1981–2010, using https://cds.climate.copernicus.eu). The mean elevation of SOPWA field sites is 116 m above sea level (range: 14–211 m above sea level). The study area lies within the forest zone of west Africa known in the phytogeographical literature as Upper Guinea, running from Sierra Leone in the west to the Dahomey Gap (Ghana) in the east, from the coast up to 350 km inland (Marshall et al., 2021; White, 1979). This area is included within the Western Guinean lowland forests ecoregion, which has been recognised as a biodiversity hotspot (Myers et al., 2000; Olson et al., 2001). Southeast Liberia is regarded as a centre of plant endemism within Upper Guinea, supporting a high concentration of globally rare species (Bongers et al., 2004; Marshall et al., 2016, 2022). The typical flora of the study area is lowland ultra-wet evergreen rainforest, characterised by species such as *Tetraberlinia tubmaniana*, *Diospyros chevalieri*, *D. sanza-minika*, *Heritiera utilis* and *Lophira alata*. Variations in species composition are driven by gradients in rainfall, disturbance and local topology, with altitude and historical climatic stability important at broader geographical scales (Marshall et al., 2022).

We collected data from 54 plots (50 × 50 m) distributed equally across three ecological systems (i) forest, (ii) country palm (iii) industrial oil palm. Plots are in six clusters, located in and around each of the six GVL oil palm plantations in Sinoe County (Tarjuowon-North, Tarjuowon-South, Butaw, Kpayan, Tartweh and Kabada) (Figure 1). There are nine plots in each cluster (three plots per system per cluster; 54 plots in total), and same-system plots within a cluster are at least 400 m apart to minimise autocorrelation. Forest plots are in areas of old-growth lowland forest, avoiding edaphic features like hilltops, slopes, swamps and significant tree falls. These areas are owned by GVL and used by local people for hunting, collecting non-timber forest products (NTFPs) and spiritual and cultural purposes. Country palm plots are on fallowed traditional farms, which community members were using to harvest oil palm fruits at the time of sampling (mean 7.6 years since farming, range 2–30 years). During the farming period, the most commonly farmed crops were rice, cassava, cucumber, pepper and bitterball. Once fallow, as at the time of the study, these areas are known locally as low bush, and support substantial vegetative regeneration of forest species. The oil palm trees are wild-growing palms from c. 8 years to 100 years old, which either survived the burning process or established naturally after farms were fallowed. Chemical fertilisers, herbicides and pesticides have never been applied within the country palm systems. Industrial oil palm plots are in GVL plantations consisting of oil palm monocultures organised into 300 × 1,000 m blocks, with palms planted approximately 9 m apart in a staggered design. Palm ages ranged from 4 to 10 years (all were fruiting at the time of the study), with 50% of plots having palms aged 6 or 7 years when we sampled. Management includes regular application of chemical and natural fertilisers, herbicides and insecticides during pest outbreaks. In comparison to country palms, industrial oil palms are high-yielding varieties supplied dominantly by PalmElit and Socfindo, with a very limited additional area planted with a Dami Mas seed test.

## 2.2 | Field data collection

We collected plant biodiversity and ethnobotanic data from February – March 2022, and vegetation structural complexity data from January – February 2023, during the regional dry season. Owing to new farms that were established by local people between our 2022 and 2023 field seasons, we moved five plots (one forest plot and four country palm plots) by <200 m to ensure they were in the same system type as the first field season.

### 2.2.1 | Tree and understorey plant biodiversity

For canopy tree data, all trees ≥ 10 cm diameter at breast height (DBH) were identified and counted within each 50 × 50 m plot,

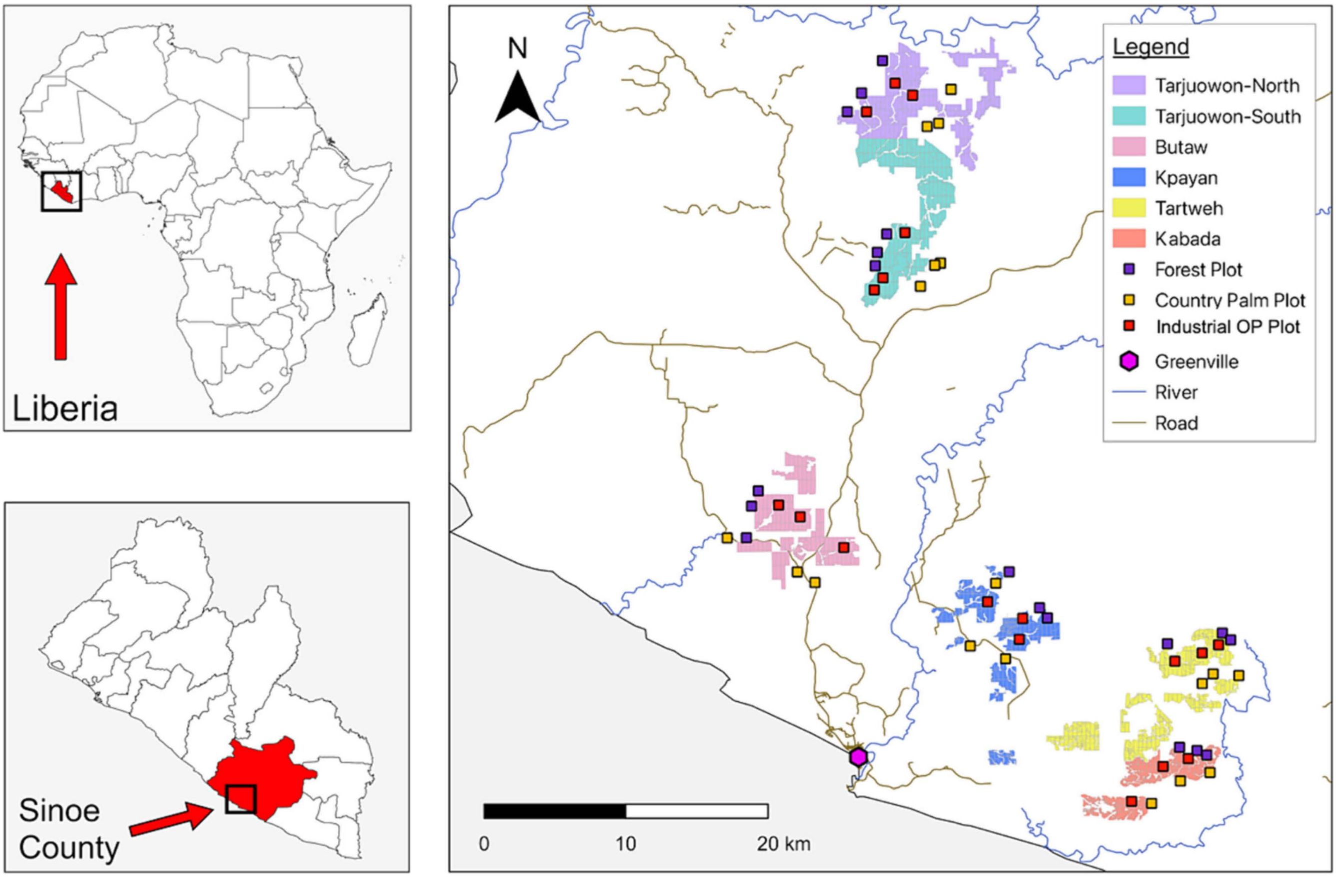


**FIGURE 1** Map of study area in Sinoe County, Liberia. We established study plots (50 × 50 m) in forest (N = 18; purple squares), country palm (N = 18; orange squares) and industrial oil palm (N = 18; red squares) systems. Our plots were spatially clustered in and around each of six industrial oil palm plantations: 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.

making use of Hawthorne and Gyakari (2006) for identification. For understorey data, a single 10 × 10 m subplot was established at one corner within each 50 × 50 m plot. In these subplots each vascular plant species present was recorded except trees ≥ 10 cm DBH (canopy epiphytic plants were not surveyed). On industrial oil palm plots herbicide is applied to palm bases and harvesting paths, affecting local vegetation and subplots were arranged randomly with respect to these patterns of herbicide application. Specimens were collected of all plants for which identification in the field was not absolutely certain. Identification followed by Hawthorne and Jongkind (2006), making use of online types available through JSTOR Global Plants. Any record carrying a synonymous name was updated to the accepted name before analysis, using the taxonomic framework of the African Plants Database (Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute Pretoria, 2016). Specimens are housed at the Forestry Training Institute of Liberia and Cambridge University Herbarium (CGE) (permit numbers in Acknowledgements). We are in conversation with the Government of Liberia to repatriate the Cambridge specimens now identification is complete. Canopy tree plot data are available in Dataset S1, and canopy tree species data are available in Dataset S2. Understorey plot data are available in Dataset S3, and understorey species data are available in Dataset S4. A species checklist is available as Dataset S5.

### 2.2.2 | Vegetation structure

We measured vegetation complexity in each plot using a terrestrial laser scanner (FARO Focus M70) (Dataset S1). Laser scans were taken at five points in each plot (at the centre point and each corner) by positioning the scanner on top of a tripod at approximately 1.3 m height. We scanned at 360° horizontally and 300° vertically with a step width of 0.035°. In theory, the Focus M70 scanner can detect objects up to 120 m away, but it generally covers a far smaller area when vegetation is present (and certainly < 200 m, the minimum distance of any plot from a different vegetation type). We imported each scan into FARO SCENE (FARO® SCENE 3D Point Cloud Software | FARO), applied standard processing algorithms and exported the resultant point clouds individually as text files. The text files condense the 3D point cloud data into a three-column dataframe that describes each scan's *x*-, *y*- and *z*-coordinates.

### 2.2.3 | Provisioning services

Before any field work began we held introductory meetings with each local community to explain our research purposes and obtain prior informed consent to research participation and publication (Cambridge Psychology Research Ethics Committee Application number: PRE.2020.004). We collected ethnobotanic data from three estates (Tartweh, Kpayan and Butaw), working with seven guides recruited from six communities (Tweh's town, Worto's town, Tubmanville, Nigeria town, Numopoh and Butaw). We recruited up to two people nominated by their communities as the most knowledgeable about plants (all men, thus our results are limited to the male population). At Butaw we were not able to collect ethnobotanic records in the three industrial oil palm plots due to the unavailability of community members during the survey days, but otherwise, all subplots ($10 \times 10$ m) were surveyed (giving a total of 9 forest plots, 9 community agriculture plots and 6 industrial oil palm plots). Ethnobotanic surveys were carried out on the understorey plots at the same time as the other understorey recording and collecting activities, so respondents gave information about all plants recorded from the subplot ('no name' or 'no use' was recorded if that was the case). We chose to bring respondents to the field to give names and use information for plant species as respondents find recognising plants in their familiar field form much easier than working from collected dried plant material. We paid a standard daily rate agreed in advance to all guides. Our guides gave local names in Kru (Tartweh and Butaw) or Sapo language (Kpayan) reflecting the dominant languages of communities living near the estates, and approximate usage notes for each understorey plant record (e.g. 'bark used to treat a cough'). The two languages were not separated during analysis due to insufficient sample replication in each language. This information was recorded for all specimens or records at the same time as they were collected. Canopy trees were not surveyed explicitly for ethnobotanic information, though many tree species were included in surveying as they were often also present as juveniles in the understorey. We carried out semi-structured interviews with informants using prompt questions: 'From which vegetation types do you collect plants?', 'What are your most important plants that you would not like to live without?', 'Do you have difficulty collecting all the plants you want?' and 'Do you take your plants to a market?'. NTFP data are reported in the species checklist, Dataset S5.

## 2.3 | Response variables

We analysed understorey and canopy data separately to understand whether the effects of management practice affected vegetation strata differently. We used only fully identified species records for analysis, with records of vague names and informal morphospecies names dropped (7% of all collected records). We allocated any identifications lower than the species level (subspecies, varieties) to the species level. Local name spellings were reviewed and standardised after specimens had been identified. We aimed for consistency and phonetic spelling, as English spellings for Sapo and Kru plant names have not yet been formalised. Use notes for each species were assigned to use categories following Level 1 of the Kew Standard (Cook, 1995).

We measured weighted endemism using the Genetic Heat Index (GHI) (Marshall et al., 2016). GHI is a continuous metric representing the inversely weighted global ranges (endemism) of the species present in a plant community so that vegetation samples with higher GHIs are home to a higher proportion of globally rare plants. The metric is similar to range size rarity or other measures of weighted endemism, except that species' ranges are measured globally at one-degree square resolution rather than within the study area at any resolution. In addition, species ranges are categorised into four groups (called Star categories) rather than being treated continuously, and the metric includes no measure of species richness, as is sometimes the case with range size rarity metrics. These modifications account for patchy distribution data associated with tropical African plants. The GHI for each sample was calculated from the species present, using the following formula, where NBK, NGD, NBU and NGN are the number of Black (globally rarest), Gold, Blue and Green Star (globally most widespread) species in a sample (with range sizes averaging 2.7, 9, 24 and > 50-degree squares respectively), and WBK, WGD, WBU and WGN are the respective weights (27, 9, 3, 0) (Equation 1).

Equation 1. GHI calculation.

$$\mathrm{GHI} = \begin{aligned} &100 \times ((\mathrm{NBK} \times \mathrm{WBK}) + (\mathrm{NGD} \times \mathrm{WGD}) + (\mathrm{NBU} \times \mathrm{WBU}) \\ &+ (\mathrm{NGN} \times \mathrm{WGN})) \div (\mathrm{NBK} + \mathrm{NGD} + \mathrm{NBU} + \mathrm{NGN}) \end{aligned}$$

We calculated two metrics of vegetation complexity: (1) *Canopy height* – the difference between the lowest and highest vertical point recorded by the scanner; and (2) *Stand Structural Complexity Index (SSCI)* – a metric of vegetation complexity. For further details of SSCI, and how we calculated this value, see (Ehbrecht et al., 2021).

## 2.4 | Analysis

We conducted statistical analyses in R 4.4.0, making use of tidyverse for data exploration; iNEXT for species accumulation curves (Figure 2c,d); vegan for fitting non-metric multidimensional scaling (NMDS, Figure 3e,f); glmmTMB and mvabund for fitting generalised linear mixed effects models (GLMM) and multivariate generalised linear models, respectively, and multcomp for post-hoc tests. We used QGIS 3.22.12 for mapping.

We used generalised linear mixed effects models (GLMM) to assess differences in plant species richness (Figure 3a,b), weighted endemism (Figure 3c,d), canopy height (Figure 4a), stand structural complexity (Figure 4b), % named and % useful (Figure 5a,b), between systems. In all GLMMs, we 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 +

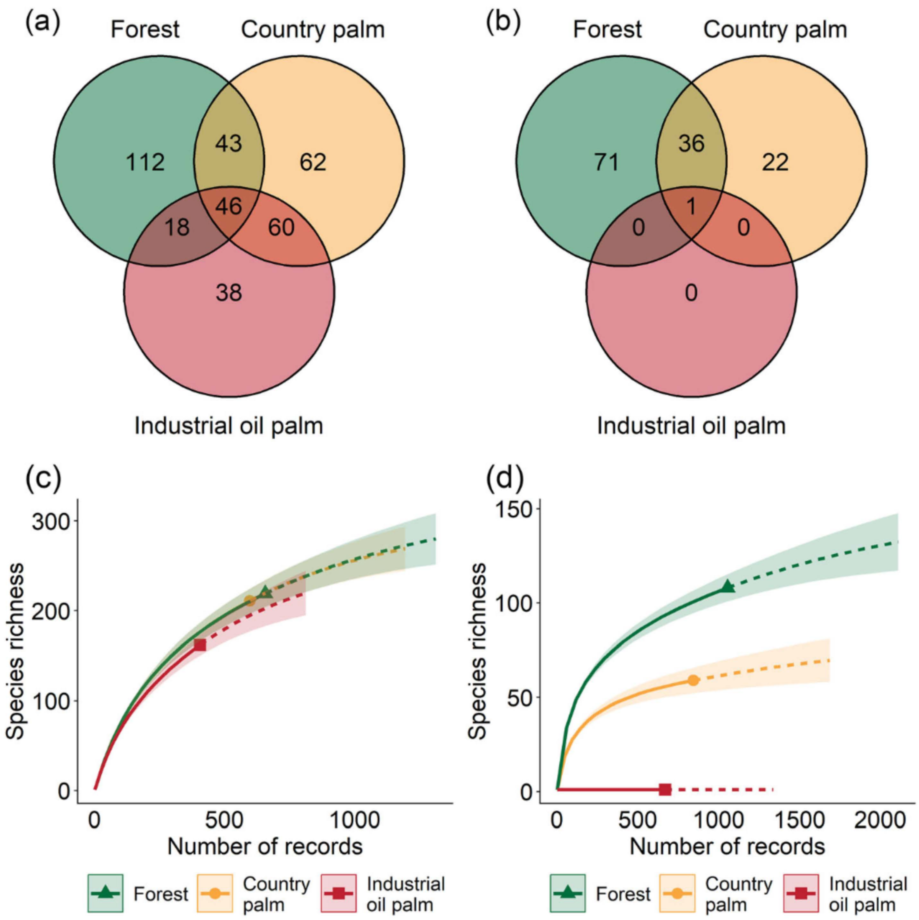


**FIGURE 2** Venn diagrams showing overlap of species between systems for (a) understorey plants; (b) canopy tree species. Numbers in circles indicate the number of species unique to each system, and numbers in areas of circle overlap indicate the number of shared species across systems. species accumulation curves for (c) understorey plants; (d) canopy trees. Shading indicates upper and lower confidence limits calculated using 2 x standard error. We plotted both interpolated (solid line) and extrapolated (dotted line) curves. We extrapolated to double the number of recorded individuals.

[1|Farm]). We fitted species richness and weighted endemism models to negative binomial distributions (log links) as Poisson-distributed models were overdispersed. For the canopy tree weighted endemism model (Figure 3d) we included only data from rainforest and country palm systems, as the industrial oil palm plot values were all 0 owing to only oil palms (*E. guineensis*, a globally widespread Green Star species) being present, leading to model convergence issues. We fitted our canopy height and SSCI models to Gamma distributions (log links), as these data were positive and continuous. We fitted % named and % useful models to beta distributions (logit links), as these data were between 0 and 1 inclusive. We validated our models by plotting Pearson residuals against fitted values and covariate *System* and verifying no patterns were present. We determined the significance of the fixed effect using likelihood ratio tests comparing GLMMs to null models; where significant we conducted pairwise post-hoc testing using Tukey all-pair comparison tests to determine differences between systems. To assess differences in species composition (Figure 3e,f), we used multivariate generalised linear models (mGLMs) with a binomial distribution for presence-absence understorey data and negative binomial distribution for counted canopy tree data, and Farm as a blocking variable. We validated the model by plotting Dunn-Smyth residuals against fitted values and covariate *System*. We determined if *System* affected the species-level composition using an LRT and by bootstrapping probability integral transform residuals using 1,000 resampling iterations. We ran univariate analyses to identify individual species with significant changes in presence (understorey) and abundance (canopy) across systems, comparing only forest and country palm systems for canopy tree data as *E. guineensis* was the only canopy tree species in industrial oil palm. Univariate *P*-values were corrected for multiple testing using a step-down resampling algorithm. We tested for an association between the use class and system using a chi-square test of association (Figure 5c).

# 3 | RESULTS

## 3.1 | Plant biodiversity

### 3.1.1 | Species richness

We made 1,599 records of 378 understorey plant species, including 219 species recorded in forest, 211 species in country palm and 162 species in industrial oil palm (Figure 2a). We made 2,162 records of 130 canopy tree species, including 108 species recorded in the forest, 59 species in country palm and just one species (*E. guineensis*) in industrial oil palm, which was found in all systems (Figure 2b). More understorey and canopy tree species were unique to the forest than any other system. Forest and industrial oil palm plots had the fewest

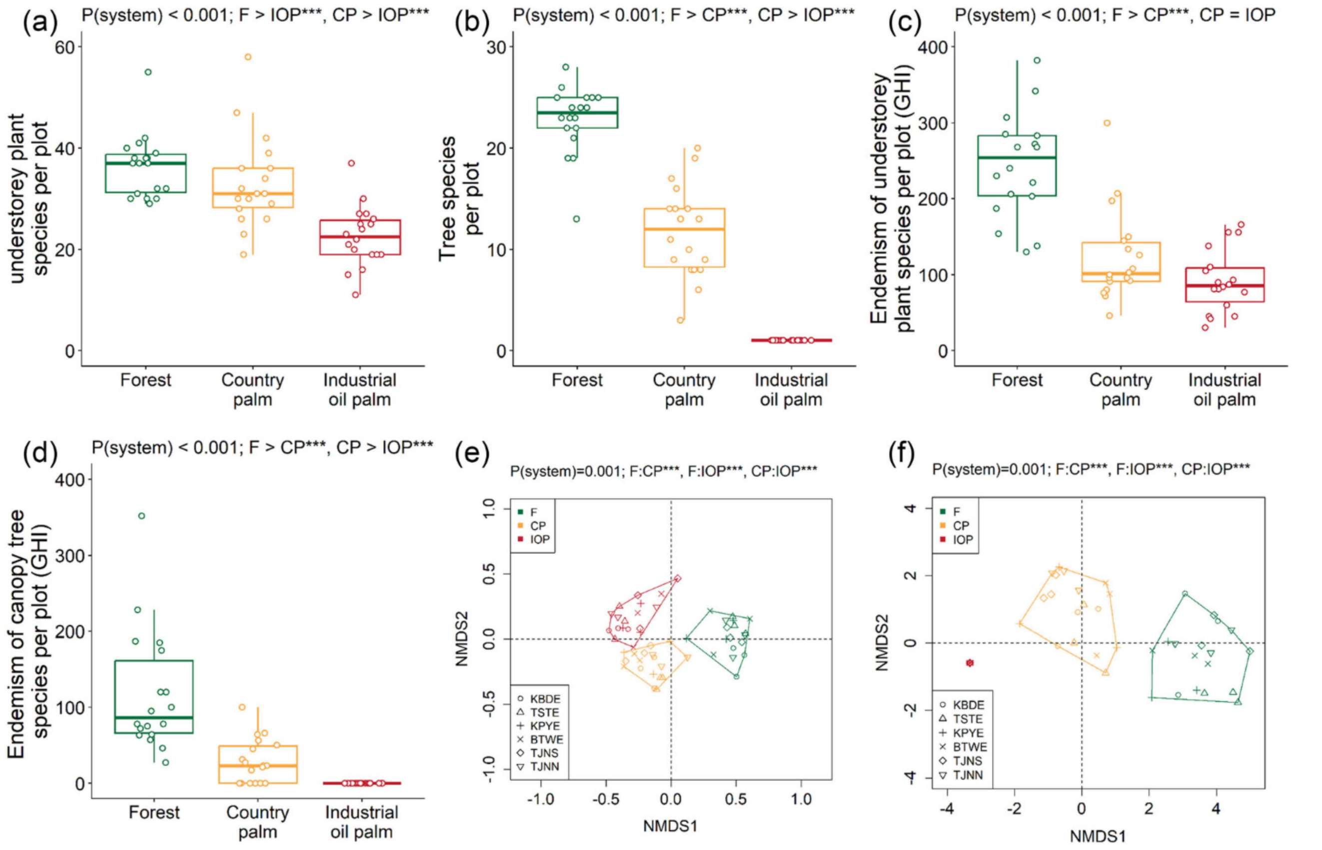


**FIGURE 3** Differences in plant biodiversity response variables across studied systems (Forest F, country palm CP, industrial oil palm IOP): (a) understorey species richness; (b) canopy species richness; (c) understorey endemism, weighted by the inverse of global range size; (d) canopy endemism, weighted by the inverse of global range size; (e) understorey community composition NMDS ordination (non-metric multidimensional scaling); and (f) canopy species-level community composition NMDS. For (a–d), the effect of *system* on each response (determined using likelihood ratio test) and results of pairwise post-hoc testing (Tukey all-pair comparison tests) are indicated above each plot: $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$. Boxplots show median (horizontal crossbar) and interquartile ranges, and circles show per-plot values. For (e–f), NMDS ordinations used a Jaccard dissimilarity matrix, specifying 3 axes; both analyses converged with stress <0.2. The effect of *system* and pairwise comparisons (determined using multivariate generalised linear models and LRTs) are indicated above each plot: $^{***}P < 0.001$. Symbols represent estate: Tarjuowon-north (TJNN), Tarjuowon-south (TJNS), Butaw (BTWE), Kpayan (KPYE), Tartweh (TSTE) and Kabada (KBDE).

species in common. Species accumulation curves in all systems were starting to plateau in the understorey (Figure 2c) and canopy (Figure 2d). The total extrapolated number of understorey species estimated for rainforest and country palm was similar (325 rainforest, 305 country palm, 269 for industrial oil palm), but highest in rainforest for canopy tree species (156 rainforest, 83 country palm, 1 industrial oil palm).

We found differences in the species richness of understorey plants per plot across systems ($LRT_{System} = 33.1$, $P_{System} < 0.001$) (Figure 3a). The average species richness of understorey plants in forest ($\bar{X} \pm SE = 36.4 \pm 1.5$) was not significantly different from that of country palm ($\bar{X} \pm SE = 33.2 \pm 2.2$), but 1.6 times greater than in industrial oil palm ($\bar{X} \pm SE = 22.4 \pm 1.4$) ($P_{comparison} < 0.001$). We found differences in the species richness of canopy trees per plot across systems ($LRT_{System} = 137.8$, $P_{System} < 0.001$) (Figure 3b). The average species richness of canopy trees in forest ($\bar{X} \pm SE = 22.8 \pm 0.8$) was 1.9 times greater than in country palm ($\bar{X} \pm SE = 11.8 \pm 1.1$); all industrial oil palm plots had only one tree species present (*E. guineensis*) ($\bar{X} \pm SE = 1 \pm 0$) ($P_{comparisons} < 0.001$).

### 3.1.2 | Weighted endemism

We found differences in the global rarity of understorey plants per plot across systems, measured using the GHI, a weighted global endemism index ($LRT_{System} = 44.0$, $P_{System} < 0.001$) (Figure 3c). The average GHI of understorey plants in forest ($\bar{X} \pm SE = 244.4 \pm 16.0$) was 2.0 and 2.7 times greater than in country palm ($\bar{X} \pm SE = 123.3 \pm 14.3$) and industrial oil palm ($\bar{X} \pm SE = 91.4 \pm 9.7$), respectively ($P_{comparisons} < 0.001$); country palm and industrial oil palm did not have significantly different GHI from each other. We also found differences in the GHI of canopy trees per plot across studied systems ($LRT_{System} = 10.9$, $P_{System} < 0.001$) (Figure 3d). All systems differed from each other, with forest ($\bar{X} \pm SE = 117.9 \pm 19.0$) having an average GHI 4.1 times greater than country palm ($\bar{X} \pm SE = 29.1 \pm 6.9$) ($P_{comparisons} < 0.01$), whilst all industrial oil palm plots had a GHI of 0 ($\bar{X} \pm SE = 0 \pm 0$).

We recorded 8 Black Star (very globally rare) species in our plots: *Dracaena calocephala* (Asparagaceae), *Glenniea adamii* (Sapindaceae), *Heterotis sylvestris* (Melastomataceae), *Leucomphalos discolor* (Fabaceae),

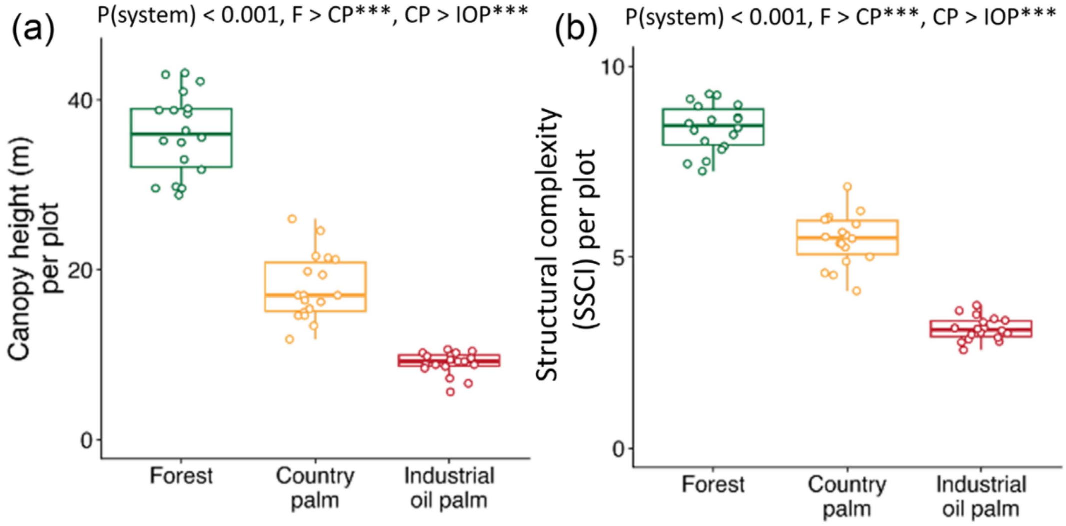


**FIGURE 4** Differences in vegetation structure response variables across studied systems (Forest F, country palm CP, industrial oil palm IOP): (a) canopy height (m); (b) stand structural complexity index (SSCI). The effect of *system* on each response (determined using LRTs) and results of pairwise post-hoc testing (Tukey all-pair comparison tests) are indicated above each plot: ****P < 0.001, **P < 0.01, *P < 0.05*. Boxplots show median (horizontal crossbar) and interquartile ranges, and circles show per-plot values.

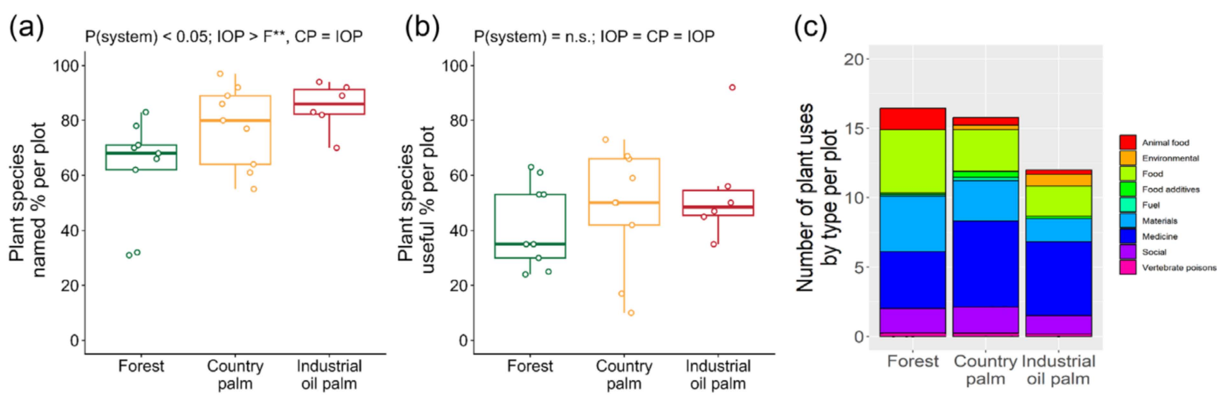


**FIGURE 5** Differences in provisioning services response variables across studied systems (Forest F, country palm CP, industrial oil palm IOP): (a) percentage of species named per plot; (b) percentage of species useful per plot; (c) number of plant uses in each use category. The effect of *system* on each response (determined using LRTs) and results of pairwise post-hoc testing (Tukey all-pair comparison tests) are indicated above each plot: ****P < 0.001, **P < 0.01, *P < 0.05, n.s. = non-significant*. Boxplots show median (horizontal crossbar) and interquartile ranges, and circles show per-plot values.

*Loesenera kalantha* (Fabaceae), *Pauridiantha liberiensis* (Rubiaceae), *Pavetta sonjae* (Rubiaceae), *Tetraberlinia tubmaniana* (Fabaceae) and *Uvaria sassandrensis* (Annonaceae). All of these species were restricted to forest plots, except for the herbaceous pioneer species *Heterotis sylvestris*, which was restricted to country palm and oil palm, the legume climber *Leucomphalos discolor*, found in a single country palm plot, and *Dracaena calocephala*, found in a single country palm plot but otherwise forest. Just outside of a forest plot in Kpayan estate, we recorded an additional Black Star species *Chassalia hallii*, as well as juveniles of the unusual carnivorous forest liane *Triphyophyllum peltatum*, one of only three monotypic genera in the family (Dioncophyllaceae), all restricted to the forests of Liberia, Ivory Coast and Sierra Leone. We found the as-yet unpublished and very rare *Octoknema* sp. A (Hawthorne & Jongkind, 2006) in the forest in Tartweh. We recorded three IUCN Red List Endangered species (*Cola boxiana* restricted to country palm, *Placodiscus pseudostipularis* restricted to rainforest, *Heterotis sylvestris* found in country palm and industrial oil palm) and a further 12 Vulnerable species.

### 3.1.3 | Species composition

We found differences in the species-level community composition of plants in the understorey across systems ($LRT_{System}$ = 2,233, $P_{System}$ < 0.001) (Figure 3e). Post-hoc analyses showed differences in species-level community composition of understorey plants between forest, country palm and industrial oil palm systems ($P_{comparisons}$ < 0.001). Univariate analyses indicated that compositional differences were driven by significant changes in the frequency of 15 species ($P_{Univariate}$ < 0.01). For example, shade-bearing species typical of the forest floor understorey like *Agelaea pentagyna* and *Cercestis afzelii* were less common in industrial oil palm; the ubiquitous fern creeper of oil palm *Nephrolepis biserrata* was more common in country palm and industrial oil palm, whilst the weedy legume creeper *Desmodium adscendens* was more common in country palm plots.

We also found differences in the species-level community composition of trees in the canopy across studied systems ($LRT_{System}$ = 1,309, $P_{System}$ < 0.001) (Figure 3f). Univariate analyses indicated that compositional differences were driven by significant changes (p < 0.01) in the frequency of 15 species ($P_{Univariate}$ < 0.001). In particular, the pioneer tree species *Macaranga barteri* and *Musanga cecropioides* were confined to country palm plots, whilst evergreen forest species *Calpocalyx brevibracteatus*, *Dialium aubrevillei* and *Diospyros sanza-minika* were only found in forest plots, and *E. guineensis* was the only canopy tree observed in industrial oil palm.

## 3.2 | Vegetation structure

We found differences in canopy height ($LRT_{System}$ = 152.4, $P_{System}$ < 0.001) and structural complexity ($LRT_{System}$ = 154.9, $P_{System}$ < 0.001) across systems (Figure 4a,b). Canopy height in forest ($\bar{X}$ ± SE = 36.1 ± 1.1 m) was 2.0 and 4.0 times greater than in country palm ($\bar{X}$ ± SE = 17.9 ± 0.9 m) and industrial oil palm ($\bar{X}$ ± SE = 9.0 ± 0.3 m), respectively ($P_{comparisons}$ < 0.001) (Figure 4a). Structural complexity in forest ($\bar{X}$ ± SE = 8.4 ± 0.1) was 1.5 and 2.7 times greater than in country palm ($\bar{X}$ ± SE = 5.5 ± 0.2) and industrial oil palm ($\bar{X}$ ± SE = 3.1 ± 0.1), respectively ($P_{comparisons}$ < 0.001) (Figure 4b).

## 3.3 | Provisioning services

Of 378 species recorded in the understorey across all subplots (N = 54), 270 species (71%) were recorded from subplots in which ethnobotanic data were also collected (N = 24). A total of 216 species were encountered on subplots surveyed by Kru respondents (N = 15), and 169 species were encountered on sublots surveyed by Sapo respondents (N = 9).

Of 270 surveyed species, 220 had names (81%), whilst 183 species had at least one use (68%). The percentage of species named differed by system ($LRT_{System}$ = 8.57, $P_{System}$ < 0.05) (Figure 5a). The highest percentage of species were named in industrial oil palm ($\bar{X}$ ± SE = 85.0% ± 2.9%), which was 1.4 times higher than the percentage named in the forest ($\bar{X}$ ± SE = 62.3% ± 6.2%, p < 0.05), but did not differ from the percentage named in country palm ($\bar{X}$ ± SE = 77.9% ± 4.9%). However, the mean absolute number of species named was lowest in industrial oil palm (16.7 ± 1.6, cf 21.9 ± 1.7 in forest and 22.4 ± 2.3 in country palm), as the species richness of this system is relatively lower. The percentage of species considered useful did not differ by the system, with forest at 42.1% ± 5.1%, industrial oil palm 54.2% ± 6.6% and country palm 48.2% ± 7.3% (Figure 5b), though the absolute number of useful species recorded was highest for forest (134) and lowest for industrial oil palm (66), again likely owing to differences in species richness between these systems. The number of uses by class was independent of the system overall (Xsq = 4.1, p = 0.99), i.e. each use class was equally well provided by each system overall (Figure 5c). More medicinal uses were recorded than any other use category (5.22 uses on average per plot), followed by food (3.2 uses) and materials (2.9 uses).

Our respondents noted that collecting plants from the forest was a job carried out by specialists, especially for medicine, whereas collecting from 'young bush' as in-country palm vegetation was a generalist activity. Our respondents agreed that they did not struggle to collect the plants they wanted in sufficient quantity or proximity. Wild-grown plants which were collected for sale in Greenville (the nearest city) included *Piper guineensis*, bush pepper, popular with the Mandingo population of Ivory Coast; and chewsticks (mainly *Garcinia* spp) which were traded with Ghanaians.

Important plants for our male respondents were associated with housebuilding, e.g. *Xylopia aethiopica* Porbueh (Kru, Sapo) and *Harungana madagascariensis* Slowen (Kru, Sapo) for poles, the Araceae climber *Cercestis afzelii* Gmonayan (Sapo), Todubu, Monkey vine (Kru, Liberian English) used as bush rope to tie house roofs and poles. Medicinal plants were used to treat a wide range of common ailments such as toothache, worms, period pains, stomach aches, snake bites, fever, cough, diarrhoea, chicken pox, to induce labour and relieve constipation in babies. The fern *N. biserrata* Gblorbo (Sapo), Jorwoloah (Kru) commonly found climbing oil palm trees was reported to be useful in treating jukes (skin punctures) from oil palm thorns. Popular wild-collected edible plants included the cauliflorous fruits of the tree *Chlamydocola chlamydantha* Kanweahtu (Kru), Karjolotueh (Sapo); the seeds of *Coula edulis* African walnut (English), Slahtu (Kru), Slahtueh (Sapo); the fruit of *Delpydora gracilis* Fankanmoneh (Kru, Sapo); various wild yam species with either root or aerial yams, e.g. *Dioscorea minutiflora* Tehdubu (Sapo), Korwen (Kru) and the lemon-scented leaves of *Neolemonniera clitandrifolia* Palm butter leaf tree (English), Palm wun tu (Kru) to flavour palm oil soups. The social use category included many plant species used to bring good luck, especially for hunting, and for personal protection against guns, cutlass wounds, snakes, lightning, witchcraft, fever, poisoning and bad luck. Animal poisons included several reported fish poisons (*Symphonia globulifera* Tokodeah (Sapo), *Mammea africana* Torkorlieh (Sapo), *Piptadeniastrum africanum* (name forgotten by respondent), a commercial *Senna* sp. Dubu (Sapo) bought as seed from Greenville for the purpose of fishing, and *Cnestis corniculata* Dobotu (Kru).

The habit of the plant was sometimes included in the plant name, i.e. tu (Kru) or tueh (Sapo) meaning tree and dubu (Kru) and dubumon (Sapo) for climber or liane. Common species sometimes share a name in Kru and Sapo e.g. *Alchornea cordifolia* Poloweh (Kru, Sapo). Species that are similar to each other may be distinguished as the male and female of a type, or mother and grandmother of a type, e.g. the two leguminous forest lianes *Duparquetia orchidacea* and *Leptoderris* *sassandrensis* were considered the female Dubukah and the male Dubukah, the former because it has more conspicuous flowers and fruits than the latter ("it can bear"); the Connaraceae climber *Agelaea pentagyna* (which resembles juvenile *D. orchidacea*) was also included in the name. The familial or generic similarity was sometimes recognised alongside species habitat preferences, with e.g. *Dracaena calocephala* Bolonyammeneh (Kru) noted as the forest type, distinct from a young bush type and a swamp type (probably of *Dracaena*, but unspecified). Kunkora (Kru) denoted secondary forest (defined by respondents as 50–100 years since clearance for farming), while Kwahjeleh (Kru) denoted high forest (at least 100 years since clearance) and foleh (Kru), farm.

## 4 | DISCUSSION

In this study, we assessed differences in the biodiversity, vegetation structure and provisioning services of plants in the understorey and canopy across the rainforest and two styles of oil palm cultivation: traditionally managed agriculture with wild-growing oil palms 'country palm', and industrial oil palm plantations, in Sinoe County, Liberia. Our study is one of the first published ecological studies in Liberia since its civil wars ended in 2003, shedding light on one of the least studied rainforest areas of Africa and how its biodiversity is influenced by agricultural activities.

### 4.1 | Biodiversity and vegetation structure

Plant biodiversity was much higher in rainforests than in industrial oil palm plantations, with traditional country palm cultivation systems having an intermediate ecological value. Though understorey plant species richness was similar for rainforest and country palm, on average the species supported by rainforest were more geographically restricted than those supported by either the country palm or industrial oil palm systems. For trees, both species richness and weighted endemism were intermediate in country palm compared with either rainforest or industrial oil palm. More globally rare species were restricted to rainforest plots than to either type of productive plots, though one very globally rare Endangered species was not found in the forest (the herbaceous pioneer *Heterotis sylvestris*), and the Endangered understorey forest tree *Cola boxiana* was found only in a country palm plot (though we would expect to find it in forest with further sampling). Overall, the three systems supported distinct plant communities from each other, with rainforest being the most valuable from a global biodiversity conservation point of view.

Time since disturbance has been found to be a significant determinant of the concentration of globally rare plants in this region (Marshall et al., 2022), which in addition to forest structure explains the decline in understorey weighted endemism from rainforest last cleared at least 200 years ago, to country palm (c. 8–100 years since clearance) and industrial oil palm systems of 4–10 years' establishment. The range of oil palm ages studied likely contributes to variability in the present dataset, as oil palm age has a marked effect on understorey cover and composition, especially before three years (Luskin & Potts, 2011). This would be interesting to quantify with a chronosequence plot setup, which we do not have at present. In Indonesia, a rubber (*Hevea brasiliensis*) cultivation system known as jungle rubber was also found to have intermediate species composition, diversity and alien species compared with either intact forest or monoculture rubber production (Rembold et al., 2017); jungle rubber is a managed agroforest system established by planting rubber trees into secondary or disturbed forest, somewhat comparable to a country palm oil palm production system. Country palm systems also had intermediate canopy heights and structural complexity compared with rainforest (higher canopies, more structurally complex) and industrial oil palm (lower canopies, less structurally complex), presumably reflecting the intermediate age of the trees at least in part. The complexity of forest structures plays a crucial role in regulating forest ecosystem functions and strongly influences (or is influenced by) biodiversity at a global scale, with hotspots of high structural complexity coinciding with hotspots of plant diversity (Ehbrecht et al., 2021). Our highest structural complexity index measure was 9.27 (in the forest, mean 8.4 for forest), equivalent to a 'hotspot of very high potential structural complexity' sensu Ehbrecht et al., 2021.

Though at lower vegetation density and less mature than would be found in rainforest, industrial oil palm understories with closed canopies supported pioneer and semi-shade-tolerant tree species typical of the rainforests of this region, such as *Alchornea cordifolia*, *Anthocleista nobilis*, *Anthonotha macrophylla*, *Bridelia grandis*, *Funtumia africana*, *Harungana madagascariensis*, *Milicia excelsa* and *X. aethiopica*, as well as typical rainforest liane species like *Manniophyton fulvum*, *Tetracera affinis* and various *Dioscorea* and *Landolphia* species, and ground flora species like *Costus afer*, *Geophila afzelii* and *Mapania linderi*. All of these species were also supported in abundance on country palm systems, along with many more species of secondary forest and some later succession species. In Indonesian oil palm plantations managed similarly to GVL (although with no rainforest in the immediate surrounding landscape), a diverse plant community of 120 species has been reported (cf. 162 species in industrial oil palm in Liberia, this study) including many native species alongside non-native species (Luke et al., 2019), particularly towards the edge of plantation blocks (30 ha size) compared with core block areas. This was attributed to greater natural reseeding rates and lower levels of harvesting disturbance such as the application of herbicides, manual cutting for paths and trampling by harvesters, suggesting a major role for reduced disturbance and herbicide use rates in supporting biodiversity within productive systems. On other industrial plantations in Indonesia, plant communities in industrial oil palm plantations were found to be very species-poor compared with forest, with trees, lianes, epiphytes and indigenous palms missing from oil palm plantations entirely (Danielsen et al., 2009). Instead, the majority of plants (and animals) in Indonesian oil palm plantations were made up of a small number of generalist species of low conservation concern. Rembold et al. (2017) also found Indonesian oil palm plantations to be characterised by a high density of herbaceous weeds, with low species numbers and low beta diversity and 25% of species (and 62% of individual plants) belonging to alien species. Industrial oil palm plantations in Liberia were also rich in globalised herbaceous dicot, grass, sedge and fern species like *Ageratum conyzoides*, *Calopogonium mucunoides*, *Centotheca lappacea*, *Cyperus cyperoides*, *Eleusine indica*, *Mimosa pudica*, *N. biserrata*, *Piper umbellatum*, *Pueraria phaseoloides* and *Solanum torvum*, all of which also occur in abundance on Indonesian oil palm plantations (Sahari et al., 2023). However, in contrast to Asian oil palm systems, Liberian plantations were not exclusively dominated by such globalised species, and only three recorded species (1.85% of total) are considered non-native to Africa (*P. phaseoloides*, *M. pudica and S. torvum*) (African Plants Database, 2024). Patterns in the SOPWA study area in Southeast Liberia are likely owing to ongoing seed rain from a large amount of old-growth forest surrounding the industrial plantations and country palm plots, and perhaps also the seed bank legacy, as industrial plantation was established here only in 2012 (the latter would be interesting to follow over the longer term). Additionally, because oil palm is native to this area and naturally forms almost monospecific stands in low-lying rainforests (though less extensive and with less dominance than in a plantation), it is plausible that native species should be more able to regenerate in commercial plantations in Liberia than is the case for Indonesian forest species.

## 4.2 | Provisioning services

Overall, 68% of surveyed species (183) were considered useful in at least one use category, with country palm and rainforest systems supplying the greatest number of useful plant species, and industrial oil palm providing the highest percentage of useful species per plot. Wild plants were used routinely in daily life, and our local guides as well as GVL staff working with us took the opportunity to collect non-timber forest products for personal use when we visited the forest. A very similar total number of useful species (228) was recorded in the Putu Hills, Sinoe County Liberia, a site c. 100 miles to the northeast (Marshall & Hawthorne, 2012). At Putu, Marshall and Hawthorne (2012) found that a significantly higher proportion of pioneers and herbaceous plants typical of disturbed and secondary vegetation were useful than shade-bearing plants typical of rainforest, but that more useful species belonged to the shade-bearing guild than any other, i.e. the same pattern of resource provisioning by habitat as in the present study. This finding is quite typical of plant use worldwide, for example, weeds are over-represented in traditional medicinal floras, but non-weeds contribute more medicines overall (Stepp & Moerman, 2001). As we found here, globally widespread plants and plants of disturbed and agricultural systems tend to be well-known and well-used locally, so that plant utilisation patterns are often at odds with patterns of plant biodiversity value, which instead emphasise species richness, diversity and scarcity as valuable plant attributes. This pattern has been identified globally, with utilised plant species richness varying inconsistently with endemism indices worldwide (Pironon et al., 2024). Documented ecosystem services provided by the plant communities of oil palm plantations in Asia include soil erosion prevention and increased soil fertility and water-holding capacity (Anderson, 2008), reduction of $CO_2$ emissions via reduction of soil temperature (Drescher et al., 2016) and reduced populations of pest species (Bedford, 1980). Complementing this knowledge base, our present study documents the importance of oil palm productive plant communities in direct provisioning services, especially for medicine, food and building materials.

We have not distinguished the two languages of our respondents (Kru, Sapo) in our analysis due to insufficient sample replication in each language. The Sapo language is part of the Kru language family (Marchese, 1983), but we acknowledge that differences could exist between these two languages in terms of plant usage and naming, in spite of their proximity and shared history. We were also not able to analyse responses by gender, as local communities always nominated men to be our respondents. However, as plant use patterns are likely to vary between male and female respondents (Dovie et al., 2008), the results reported here are likely to apply only to the male Kru and Sapo population.

## 4.3 | Implications for conservation and management

The intermediate ecological value of country palm systems is important for informing the management of industrial oil palm plantations for better ecological outcomes, for example, choice of cover crop. Our local guides identified *P. phaseoloides*, simply called Cover Crop (Kru, Sapo), as a species brought by GVL which had not been present in the area previously. Native to Asia, this nitrogen-fixing legume species with a smothering habit has become very widespread around the concession since its introduction by GVL. It has been used as a cover crop for oil palm and rubber cultivation in west Africa for decades and is recognised as a noxious weed across the American and African tropics (Rojas-Sandoval & Acevedo-Rodríguez, 2013). The equivalent niche in country palm productive systems is occupied by the legume *D. adscendens*, a native (though still globally widespread) cover crop useful as fodder, compost and medicine (Burkhill, 1985; Manzione et al., 2022). Our respondents reported it to be a useful treatment for stomach bloating and diarrhoea. *D. adscendens* would be preferable from a conservation perspective as a cover crop in west African industrial oil palm plantations owing to its nativeness and local uses. A study comparing the relative merits and impacts of *D. adscendens* as a cover crop for oil palm plantations in west Africa should be undertaken, as it has been for banana plantations in Côte d'Ivoire (Kosso Boka et al., 2022). There may also be relevant trial data in the grey literature from the early years of oil palm development.

Another possibility raised by traditional country palm cultivation systems is intercropping and agroforestry on industrial oil palm plantations, with locally desirable crop species like rice and bitterball potentially cultivatable before canopy closure (Namanji et al., 2020). This would be much closer to the traditional farming system, where mature oil palm trees co-exist with crops grown on a fallow rotation, spontaneous NTFP species and other productive wild species spared from clearance. This could alleviate any reduction in access to wild foods associated with the loss of forests and increase the resilience of food production in industrial plantations. In Malaysia, oil palm alley-cropped with secondary crops like pineapple and black pepper has been show to increase arthropod order richness, abundance and ecosystem services compared with monoculture oil palm (Ashraf et al., 2018), perhaps as a result of having more heterogenous understories (Azhar et al., 2015). Managing for increased understorey vegetation complexity on industrial oil palm plantations would likely lead to overall increases in biodiversity and ecosystem functioning, more similar to that of the country palm production system, and with negligible reduction in yield except in exceptional drought years, as in Indonesia (Hood et al., 2020; Luke et al., 2019). Understorey vegetation of industrial oil palm in GVL farms in Liberia is already a valuable habitat for predatory insect and arthropod species, which can control insect pests of oil palm (Stone et al., 2023). Even under closely-spaced (9 m) commercial planting designs as established by GVL, shade-tolerant and locally commercially important plant species like *Piper guineense* (bush pepper), *Garcinia afzelii* and *Garcinia kola* (chew-sticks, bitter cola) and *Cola nitida* (cola nut) could flourish and many other NTFP species reported in this publication could be screened for compatibility and non-competition with mature oil palm trees. Intercropping with locally valued crops or wild plants could enhance the contribution of industrial oil palm production to local food security and the local economy, as well as biodiversity and ecosystem functioning.

It is important to consider the ecological footprint of alternative land use options from converting rainforest to industrial oil palm in Liberia, a country seeking to increase its economic potential and improve livelihoods for its people. Our forest plots were within GVL land, where High Conservation Value (HCV) and High Carbon Stock (HCS) forests have been maintained for conservation purposes. Industrial rubber plantations, such as that at Firestone (Margibi County), are not likely to have higher ecological or social value than oil palm production (Rembold et al., 2017). The traditional use of forest is shifting agriculture, where the forest is cleared, cropped, then left for a fallow period, alongside protecting forests for the collection of forest products and social functions such as Poro or Sande rituals. Though shifting agriculture can be sustainable over the long-term, increasing population pressure and climate change is likely to make this increasingly unsustainable. While country palm plots had higher biodiversity than industrial oil palm plantations, industrial oil palm plantations are likely to produce far higher yields per hectare, due to improved seed stock and high rates of application of fertilisers. Producing an equal supply of palm oil for the global economy via the traditional country palm system would therefore likely require further rainforest conversion. In addition, as traditional country palm systems still have negative impacts on biodiversity compared with rainforests, the overall environmental footprint of that scenario would likely be higher. However, country palm should remain a part of the Liberian landscape for its social and cultural importance and role in local food security and economy. Country palm systems should also be used as a blueprint to inspire more ecologically and culturally appropriate farming on existing (not expanded) industrial oil palm plantations in west Africa, such as using native cover crop species and intercropping with locally valued crops and wild plants. Whether such measures would reduce industrial yields in Liberia remains to be quantified, and the trade-offs may be complex. In terms of global food security, reductions in industrial yield, justified in terms of benefits to nature, could be compensated by an increased cost of palm oil to the consumer, perhaps marketing the resultant foodstuffs as a high-value commodity. Or, reduced yields could be compensated by reductions from the demand side, for example by removing oil palm from the biofuel industry (c. 5% of total consumption, Noleppa & Cartsburg, 2016), reducing reliance on ultra-processed foodstuffs by improving access to fresh foods and reducing food waste. An alternative from a global food perspective would be for industrial production to remain concentrated in less biodiverse temperate areas, though this solution would do nothing to boost Liberian economic output. Although this would require more land for the same yield (c. 2.5 times more for rapeseed than oil palm, Meijaard et al., 2020), it could result in lower ecological impacts overall given the lower species richness of temperate regions. In practice, the best decision on a global scale is likely to require careful weighing up of costs and benefits in terms of biodiversity loss, production and economic and social benefits for individual countries.

Our study highlights potential improvements in the ecological and social value of oil palm production that could be achievable in Liberia and further afield in west Africa by altering management practices, in particular by incorporating lessons from traditional production systems. To this end, we recommend

- A comparison of the effects of native *Desmodium adscendens* vs non-native *Pueraria phaseoloides* as a cover crop for oil palm cultivation in west Africa;
- Screening locally-valued crop and wild plants reported in this study for compatibility and non-competition with oil palm trees at different stages of maturity in intercropping field trials;
- Quantifying oil palm yields and costs per hectare in industrial vs traditional production systems.

If successful, such interventions could enhance the contribution of industrial oil palm production to local food security and the local economy alongside global food production, as well as enhancing the biodiversity and ecosystem functioning of industrial production systems.

## AUTHOR CONTRIBUTIONS

CAMM led field data collection with assistance from MMG, MDP, PMH, MTJ, TJ and AS. CAMM identified the understorey plants. MMG identified the canopy trees. CAMM and MDP led statistical analyses. CAMM wrote the manuscript with contributions to the text from BF, J-P C, ECT and MDP. RW, J-PC, AS, TJ and WD provided significant administrative support to the SOPWA project. MDP leads the SOPWA project.

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## CONFLICT OF INTEREST STATEMENT

Co-authors with a Forestry Development Authority (FDA), Golden Veroleum Liberia (GVL) and Sinar Mas Agro Resources and Technology Research Institute (SMARTRI) affiliation were employed by their respective institutes and companies while research was conducted. The University of Cambridge retains all intellectual property rights and data use rights. This research is a collaboration between all affiliated parties.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

## ETHICS STATEMENT

We thank the Government of Liberia for permission to conduct our research (Republic of Liberia Business Visa #910), and the FDA for permission to collect (permit number: MD/022/2022/−4) and export (permit number: MD/048/2022/−1) specimens. Permission to conduct fieldwork was also obtained from GVL and from local communities. Prior informed consent to conduct informal interviews, record and publish ethnobotanic data was given by community members; protocols were reviewed and approved in advance by the Cambridge Psychology Research Ethics Committee (PRE.2020.004, amended January 2022). No CITES-listed species were exported. Specimens received a phytosanitary certificate from the Ministry of Agriculture before export (certificate number RL/MOA/DTS/NQES/031822/DCM-10).

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## SUPPORTING INFORMATION

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