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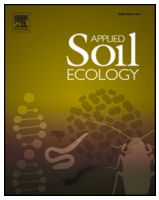

Research paper

Changes in soil-root-organism interactions following tropical forest conversion to tree and oil palm plantations

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ABSTRACT

The impacts of monoculture establishment on tropical ecosystems and biodiversity have been the subject of extensive studies, yet the impact on the relationship between soil, plant root, and organism has received limited attention. We sought to assess changes in soil-root-organism interactions resulting from tropical forest conversion to monocultures. Using data from forests and multiple tree and oil palm plantations in Indonesia, we found that the conversion of forests to monocultures impacted soil ecology through direct and indirect effects on soil physicochemical properties, root exudates, and soil organisms. Land management practices and plant physiology influenced soil physicochemical properties across land use types. While root exudates of primary metabolites associated with plant growth were strongly related to soil physicochemical properties, both soil physicochemical properties and the underlying ecological differences between forests and monocultures play important roles in determining secondary metabolite exudates responsible for plant-plant interface, including competition and defence against pathogens. This demonstrates that secondary metabolites evolve through a complex mechanism involving both physical processes and interactions with other plants. Despite having superior primary and secondary metabolites responsible for competition, monoculture plantations had weaker defensive metabolites for pathogen suppression than forests. Furthermore, monocultures had a significantly higher proportion of fungi in their soil microbial profiles than forests. A weakened defence system, combined with elevated fungal presence, can increase monocultures' susceptibility to disease. Our results underscore the critical role of diverse ecosystems in ensuring ecological stability, emphasising the necessity for enhanced diversity in monocultures, whether through agroforestry or intercropping, for long-term soil health.

1. Introduction

Tropical forests have been rapidly reduced in size and converted to monoculture plantations to meet agricultural commodity demands for oil palm, rubber, and pulpwood (Hoang and Kanemoto, 2021; Fagan et al., 2022). Since 2000, 32 million hectares of monoculture plantations have been established pantropically (Fagan et al., 2022). Plantations specialise in a few crops regionally, with Southeast Asia cultivating oil palm, rubber, and acacia; Latin America focusing on oil palm, eucalypt, and pine; and Africa in the early stages of oil palm development (Fagan

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et al., 2022). Approximately 45 % of oil palm plantations established in Southeast Asia over the last decades were allegedly developed by displacing natural forests. In the last 20 years alone, >52,000 km^2 of tropical forests in this region, mostly in Laos, Myanmar, and Southwest China, have been converted into rubber plantations (Fox and Castella, 2013; Zhang et al., 2019). With the growing threat of climate change, tree plantation projects have gained traction as part of the global effort to achieve net zero emissions (Van Kooten and Johnston, 2016; Essl et al., 2018). Commercial tree monocultures are thriving in tropical regions, aided by financial incentives from the private and public sectors for carbon offsetting programs, which typically aim to increase aboveground carbon through woody biomass (Aguirre-Gutiérrez et al., 2023). Acacia, eucalyptus, and pine trees are attractive for this purpose since they can grow considerably faster in the tropics than in their native environments in drier or higher latitude areas (Griffin et al., 2011; Dodet and Collet, 2012).

The conversion of multi-strata tropical forests to monoculture has been shown to have serious implications for climate, ecosystems, and

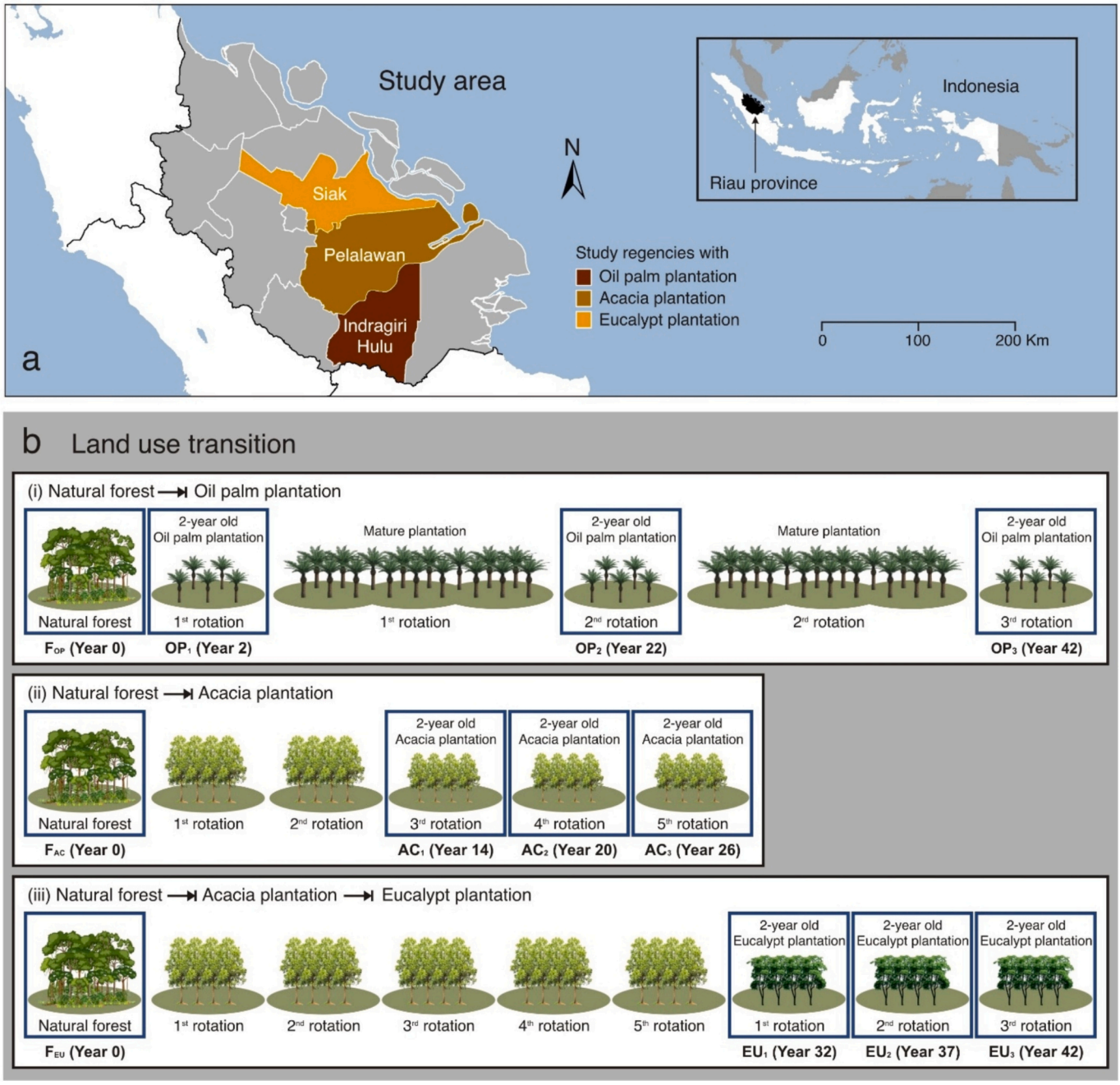

Fig. 1. Study area and land use transitions evaluated. (a) Study regencies in Riau province of Indonesia where the three plantations occurred, including Indragiri Hulu regency for the oil palm plantation, Pelalawan regency for the pulpwood plantation with the *Acacia mangium* species, and Siak regency for the pulpwood plantation with the *Eucalyptus pellita*. (b) Schematic diagram of the different land uses evaluated (blue square) associated with the three plantations and the historical land use pathways. These include: (i) the change from natural forest at year 0 (F_{OP}) to oil palm plantation at year 2, 22 and 42 for the first (OP_1), second (OP_2) and third rotation (OP_3), respectively; (ii) the change from natural forest at year 0 (F_{AC}) to acacia plantations at year 14, 20, and 26 for the third (AC_1), fourth (AC_2), and fifth rotation (AC_3), respectively; and (iii) the change from natural forest at year 0 (F_{EU}) to acacia plantation at year 1–30 then to eucalypt plantation at year 32, 37, and 42 for the first (EU_1), second (EU_2), and third eucalypt rotation (EU_3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

biodiversity (Bradshaw et al., 2009; Seymour and Harris, 2019). Nonetheless, little study has been undertaken to determine how the introduction of plant monocultures at the expense of tropical forests and natural regrowth affects the interactions between soil, plant root, and soil organisms, as well as the possible long-term repercussions for soil health (Aguiar et al., 2014; Wells et al., 2023). Crop-specific land management regimes, such as planting density and fertiliser applications, are usually introduced once monoculture plantations are established to boost crop yields and productivity (Zhao et al., 2018; Lin et al., 2019). These land management practices can alter soil physicochemical properties, root exudates, and microbial communities (Wang et al., 2017). Furthermore, root exudates of alien plant may differ in the composition from the native soil environment, affecting the structure and function of indigenous soil communities (Cook-Patton and Agrawal, 2014; Li et al., 2022). For example, soil sugar serves as an energy source for microbes (Gunina and Kuzyakov, 2015; Widyati et al., 2022a), and excessive sugar exudate concentrations from alien species can promote pathogen proliferation in soils (Ren et al., 2020). Exudate compounds such as glucosinolates play an important role in protecting plants from herbivores and pathogens (Tsunoda et al., 2017; Hu et al., 2018), and low levels of this metabolite can increase plants' susceptibility to disease (Redovniković et al., 2008; Widyati et al., 2022b). When a monoculture plantation is harvested or cleared, its organic matter, allelopathy microorganisms, and pathogens remain in the soil ecosystem, which might affect future plant growth (Del Fabbro and Prati, 2015; Oliver et al., 2021).

In this study, we sought to analyse the soil-root-organism interactions associated with the conversion of tropical forests to monoculture plantations, while accounting for different land management regimes and plant physiological features. We examined data from Indonesia, focusing on forests and monoculture plantations of oil palm, acacia, and eucalyptus at different stages of their rotational cycles (Fig. 1). Since the 1980s, these three species have played a central role in the extensive transformation of primary forests in Indonesia into monocultures. Three components of soil ecology were investigated: soil physicochemical properties, plant root exudates, and soil organisms. We sought to answer three related questions (represented in Fig. 2): (1) How do soil physicochemical properties vary between land uses, especially between natural forest and multiple monoculture plantations, and how do these variations relate to land management practice and plant physiology? (2) How do plant root exudates (including primary metabolites responsible for plant growth and secondary metabolites responsible for plant interaction with other species) vary between land uses, and how do soil physicochemical properties alter plant root exudates? (3) How do soil organisms, including microbes and macrofauna, respond to changes in soil physicochemical, and how can root exudates alter their composition? By answering these questions, we bring light on the intricate interplay of soil, root, and organisms in various land uses. Drawing from the findings, we offer recommendations for how monoculture plantations can be modified to improve the sustainability and health of tropical soils and promote more resilient ecosystems.

2. Methods

2.1. Study area and characteristics

The research was carried out in the province of Riau, one of the main locations for agro-industrial plantations in Indonesia (Fig. 1a). Located in the humid tropical region, Indonesia has very intensive weathering of soils due to periodic heavy rainfall. Acidic mineral soils such as Oxisols and Ultisol are common, and organic matter accumulation in swampy ecosystems resulted in peat soils or Histosols. Many physical and chemical constraints exist for these three broad soil types (Tan, 2008; Du et al., 2020).

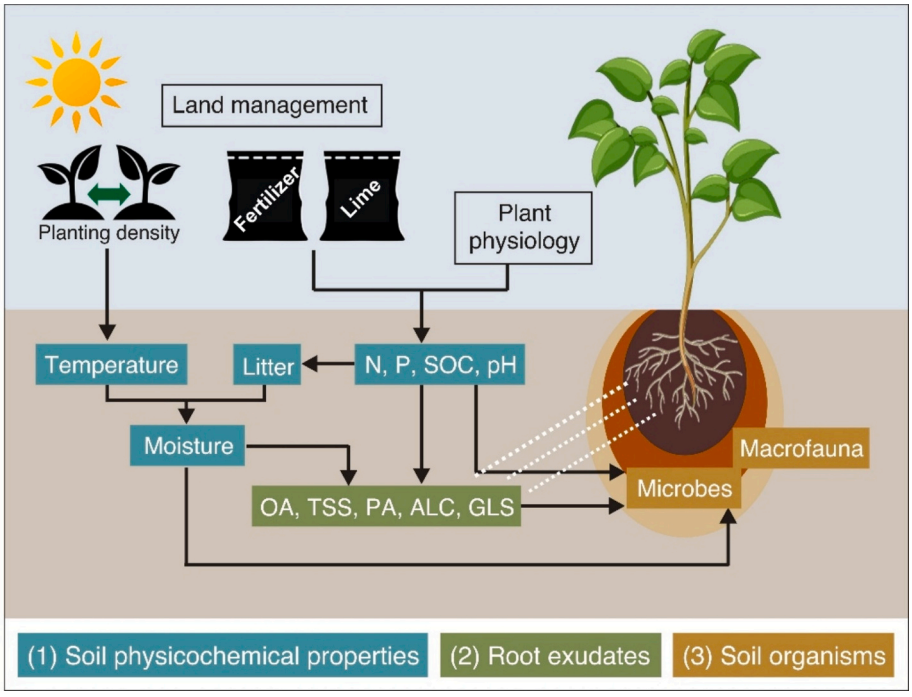

Fig. 2. Schematic diagram representing the three analysis foci undertaken, including (1) soil physicochemical properties in different land uses and their relation to land or plantation management and plant physiological features, (2) root exudate profiles in different land uses and their responses to soil physicochemical properties, and (3) soil organisms in different land uses and their responses to soil physicochemical properties and root exudates. Indicators for soil physicochemical properties evaluated include soil temperature and moisture, litter thickness, soil total nitrogen (N), phosphorus (P) availability, soil organic carbon (SOC), and pH. Root exudate compounds evaluated include organic acids (OA), total soil sugars (TSS), phenolic acids (PA), allelochemicals (such as terpenes, alkaloids, and phenols) (ALC), and glucosinolates (GLS). Soil organism indicators assessed include the abundance of microorganisms in the rhizosphere, such as bacteria, fungi, and actinomycetes, as well as the abundance of soil macrofauna, such as nematodes, annelids, and arthropods.

Plantations in Riau are primarily composed of pulpwood and oil palm (*Elaeis guineensis*). Three species are commonly found on pulpwood plantations: *Acacia mangium*, *Eucalyptus pellita*, and *Acacia crassicarpa*. *Acacia crassicarpa* is cultivated on peat soil, but *Acacia mangium* is grown on mineral soil (Harwood and Nambiar, 2014). A distinguishing feature of the acacia species, compared to oil palm and eucalyptus, is their ability to fix nitrogen in the soil through a symbiotic relationship with nitrogen-fixing bacteria (Wibisono et al., 2015). Over the past ten years, the pulpwood industries located on mineral soil have progressively shifted their attention from acacia to eucalypt species (Nambiar et al., 2018). This is due to the acacia trees' susceptibility to diseases, which are mostly caused by the Ganoderma root fungus and Ceratocystis spp. stem-wilt canker (Anthony Ba, 2004; Francis et al., 2014; Harwood et al., 2015).

In Indonesia, oil palm plantations typically follow a 20-year plantation rotation in which older trees are felled and replaced with younger ones (Ismail and Noor Mamat, 2002). Eucalyptus and acacia tree plantations typically have a much shorter rotation period of 5–6 years (Harwood and Nambiar, 2014). Both trees grow rapidly, climbing at a rate of 3–4 m per year, and can reach a height of 15–20 m at the end of the plantation cycle (Hegde et al., 2013; Prasetyo et al., 2017). These contrasting growth rates and cycle lengths necessitate distinct land management approaches for each type of plantation. Specifically, oil palm plantations are characterised by wider spacing between trees and a greater dependency on chemical inputs such as fertilisers and pesticides to maintain productivity (Gérard et al., 2017; Darras et al., 2019). In contrast, pulpwood plantations emphasise higher planting densities to maximise yield within a shorter time frame, while simultaneously maintaining lower levels of chemical inputs (Hardiyanto et al., 2021).

2.2. Soil sampling

Field surveys were conducted during the dry season of June–July 2019 in three adjacent regencies in Riau province, including Indragiri Hulu for the oil palm plantation, Pelalawan for the *Acacia mangium* plantation, and Siak for the *Eucalyptus pellita* plantation (Fig. 2a). All of these plantations were grown on mineral soil, specifically red-yellow Podzolic (Ultisol) soil. Climate conditions are similar across the three regencies, with a long-term mean annual temperature of 26.3 °C and mean monthly rainfall during the dry and wet seasons of 186.6 mm and 247.9 mm, respectively.

The oil palm plantation under investigation was previously a primary forest. The acacia plantation had previously been a secondary forest, whereas the eucalypt plantation was previously an acacia plantation that had been established in a secondary forest. The original land conditions prior to forest clearance and the establishment of plantations are represented by the forest areas set aside for conservation adjacent to each plantation. Measurements of soil fertility, root exudation, and biological fertility indicators across the three conservation forests revealed no significant differences (Table S1), indicating that pre-conversion land and soil conditions were comparable among the plantation sites. This uniformity in initial conditions provides a robust foundation for the comparative analysis of land-use trajectories across these areas.

Soil samples were collected for each plantation from four distinct locations, each of which represented a different land use and time period following the conversion of natural forests to plantations (Fig. 2b). For **oil palm plantations**, these include: (1) natural forest set aside for conservation within oil palm concession boundaries (namely F_{OP}); (2) new oil palm plantation, i.e. two years after the conversion of natural forest (OP_1); (3) second oil palm rotation, i.e. natural forest followed by 20 years of oil palm plantation (one plantation rotation) then followed by two years of oil palm plantation (OP_2); and (4) third rotation, i.e. natural forest followed by 40 years of oil palm plantation (two plantation rotations) then followed by two years of oil palm plantation (OP_3). For **acacia plantations**, these include: (1) natural forest set aside for conservation within acacia concession boundaries (namely F_{AC}); (2) third acacia rotation, i.e. natural forest followed by 12 years of acacia plantation (two acacia rotations) then followed by two years of acacia plantation (AC_1); (3) fourth rotation, i.e. natural forest followed by 18 years of acacia plantation (three acacia rotations) then followed by two years of acacia plantation (AC_2); (4) fifth rotation, i.e. natural forest followed by 24 years of acacia plantation (four acacia rotations) then two years of acacia plantation (AC_3). For **eucalypt plantations**, these include: (1) natural forest set aside for conservation within eucalypt concession boundaries (namely F_{EU}); (2) new eucalypt plantation, i.e. natural forest followed by 30 years of acacia plantation (five acacia rotations) then followed by two years of eucalypt plantations (EU_1); (3) second eucalypt rotation, i.e. natural forest followed by 30 years of acacia plantation (five acacia rotations) then followed by 5 years of eucalypt plantation (one eucalypt rotation) then two years of eucalypt plantation (EU_2); (4) third rotation, i.e. natural forest followed by 30 years of acacia plantation (five acacia rotations) then 10 years of eucalypt (two eucalypt rotations) then two years of eucalypt plantation (EU_3).

2.3. Soil analysis

Three different analyses of the soil were performed: (1) soil fertility, (2) root exudation, and (3) biological fertility. Soil fertility was assessed using indicators of soil physical properties (temperature, moisture, and litter thickness) as well as chemical properties (total nitrogen (N), available phosphorus (P), soil organic carbon (SOC), and pH). Root exudate metabolites in the soil rhizosphere were used to determine the root exudation profile. They include primary metabolites, such as organic acids (OA) and total soil sugars (TSS), and secondary metabolites, such as phenolic acids (PA), allelochemicals (including terpenes, alkaloids, and phenols) (ALC), and glucosinolates (GLS). Primary metabolite contributes directly to the growth and maintenance of cellular function in plants. Secondary metabolite, on the other hand, primarily contributes to ecological functions such as attraction, inhibition, competition, defence, and interaction with other organisms (Hu et al., 2018; Escolà Casas and Matamoros, 2021). As indicators of soil biological fertility, we used the abundance of microbes (overall bacteria, actinomycetes, and fungi) and pathogenic fungi in the rhizosphere, as well as the abundance of soil macrofauna (nematodes, annelids, and arthropods).

Five sampling plots were chosen at random for each forest or plantation site. Soil physical assessment was then performed at four randomly selected locations within each plot's square meter, including evaluation of soil temperature, moisture, and litter thickness. Using a thermo-hygrometer, we measured the temperature and moisture content of the soil, and a ruler was used to measure the thickness of the litter. To assess the soil chemical contents, root exudate profile, and soil microorganisms, approximately 1 kg of free-root soil samples were collected in the rhizosphere at four different depths ranging from 0 to 30 cm. Soil samples were then transported in cooler boxes to the laboratory for analysis.

The root exudate profile was examined using the gas chromatography coupled with mass spectrometry (GC–MS) (Escolà Casas and Matamoros, 2021). Rhizosphere soil samples were extracted in a 1:5 ratio with methanol. The extraction procedure was performed using a shaking method, where 40 g of soil were mixed with 200 mL of methanol. The soil-methanol solution was transferred into a 500 mL Erlenmeyer flask and placed on a shaker, where it was agitated at a speed of $<$100 rpm for 72 h. Subsequently, the solution was concentrated by evaporation using a rotary evaporator. A 1 μL of the sample was injected into the gas chromatograph (Agilent GC 6890 with 7683B Autosampler) in a splitless mode. The GC instrument was equipped with a fused-silica Rxi-5Sil MS capillary column (30 m, 0.25 μm film). The injector port and transfer line temperatures were set to 250 °C and 290 °C, respectively. The gas flow rate was 1 mL/minute, and the column temperature was

held for 5 min at 35 °C, followed by 35–300 °C at 10 °C/min, and then held isothermal for 20 min. The column end was fed into a sector mass spectrometer (LECO Pegasus 4D). The mass spectra acquisition rate of the instrument was 10 spectra/s, with a mass range of 50–1000 amu. The mass spectra and chromatograms were analysed using the Agilent ChemStation software. The metabolites were then identified by comparing them to data in the GC–MS library.

Microbial and fungal activities were assessed using the plate count method. A 10 g soil sample was suspended in 90 mL of a 0.85 % NaCl solution. Subsequently, 1 mL of this suspension was serially diluted in 9 mL of salt solution through seven dilution steps. From the last three dilution levels, 1 mL of each dilution was cultured on appropriate media (nutrient agar for microbes and potato dextrose agar for fungi) and incubated for 3 to 7 days. The growing colony was morphologically identified and calculated through microscopic examination, and the result was then multiplied by the degree of dilution factor. Although this culturing approach may not capture the whole breadth of microbial diversity, it is considered appropriate for comparing the functional diversity of soil in different land uses (Demko et al., 2021; Lee et al., 2021).

Soil macrofauna populations were examined at four different spots within the square meter of each plot using a trapping method. The trap was installed by digging the soil at a depth of 50 cm, and then a bottle filled with 70 % alcohol was placed inside the hole. Following that, a funnel was placed on the bottle, aligned with the soil surface. The bottle was taken after 24 h, and the macrofauna trapped inside were identified and counted.

2.4. Statistical analysis

Our data analysis focused on three broad analysis foci that corresponded to the three research questions that we aimed to answer: (1) soil physicochemical properties, (2) root exudates, and (3) soil organisms (Fig. 2). **The first analysis** goal was to determine how soil physicochemical properties varied between forests and plantations, and how they were influenced by internal factors, such as plant physiological traits, as well as external factors, such as land management. **The second analysis** goal was to assess how root exudate profiles differed across land uses and how these exudates responded to changes in soil physicochemical properties caused by internal and external factors. Finally, **the third analysis** goal was to assess how the abundance of soil organisms varied across land uses and how this variation related to soil physicochemical properties and root exudate compounds. Statistical analyses and graphical visualisations were performed using R software (version 4.2.3).

2.4.1. First analysis: Soil physicochemical properties

Variations in soil physicochemical properties between plantations and set-aside forests were analysed using an Ordinary Least Squares (OLS) regression, with an ANOVA test conducted to assess statistical significance, i.e.

$$PHYCHEM_{k,j} = \alpha_{0,k,j} + \alpha_{1,k,j}\, PLANT_{k,j} \quad (1)$$

$\forall\, k \in$ {OP, AC, EU} and $j \in$ {N, P, SOC, PH, TEMP, MOIST, LITTER}. where *PLANT* is a binary variable set to 1 for plantations and 0 for forests, while the parameter $\alpha_{1,k,j}$ indicates the difference in soil physicochemical type j between plantation type k and the forests adjacent to the plantation. Significant value of $\alpha_{1,k,j}$ indicates that the plantations have soil physicochemical properties that are significantly different than the adjacent forest area.

2.4.2. Second analysis: Plant root exudates

To evaluate the differences in root exudates between plantations and forests, we applied an Ordinary Least Squares (OLS) regression model and conducted the corresponding ANOVA test, i.e.

$$EXUDATE_j = \beta_{0,k,j} + \beta_{1,k,j}\, PLANT_{k,j} \quad (2)$$

$\forall\, k \in$ {OP, AC, EU} and $j \in$ {OA, TSS, PA, ALC, GLS}.where *PLANT* is a binary variable with the value of 1 for plantations and 0 for forests, while $\beta_{1,k,j}$ indicates the estimated difference in root exudate type j between plantation type k and the neighbouring forests.

To estimate the effect of soil physicochemical indicators on each exudate metabolite, we fitted a Generalised Additive Model (GAM) to the data, utilising the mgcv package in R (Wood, 2015). GAM was chosen because of its flexibility in fitting non-linear data while maintaining a high level of interpretability (Wood et al., 2022). Since many of the soil physicochemical indicators are highly correlated to each other (Fig. S1a), we focussed on three uncorrelated key predictors, including soil total N (N_j), P availability (PAV_j), and soil moisture ($MOIST_j$), as well as the differential baseline ecological feature between natural forests and plantations (LU_j), i.e.

$$EXUDATE_j = \gamma_{0j} + \gamma_{1j}\, LU_j + f_1(N_j) + f_2(PAV_j) + f_3(MOIST_j) \quad (3)$$

for $j \in$ {OA, TSS, PA, ALC, GLS}.

Parameters γ_{0j} and γ_{1j}, and smoothing functions f_1, f_2, and f_3 were estimated from the GAM algorithm. Because climate conditions in the three plantations were similar (Table S1), soil properties that are affected by weather conditions, such as soil moisture and temperature, are expected to be similar after controlling for other environmental factors. The contribution of each predictor variable in Eq. 3 in explaining variations in the root exudate was estimated by comparing the deviance of the full model and the reduced model that excluded the variable of interest.

2.4.3. Third analysis: Soil organisms

To evaluate the difference in soil organisms between monoculture plantations and the neighbouring forests, we applied an Ordinary Least Squares (OLS) regression model, with statistical validation provided through ANOVA, i.e.

$$ORG_{k,j} = \delta_{0,k,j} + \delta_{1,k,j}\, PLANT_{k,j} \quad (4)$$

$\forall\, k \in$ {OP, AC, EU} and $j \in$ {microbe abundance, fungi abundance, fungi share of total microbes, macrofauna abundance}.where *PLANT* is a binary variable with the value of 1 for plantations and 0 for forests, while the parameter $\delta_{1,k,j}$ indicates the difference in soil organism type j between plantation type k and the forests adjacent to the plantation.

We used GAM to estimate the effect of soil physicochemical indicators and exudate metabolites on each type of soil organisms. Because many soil physicochemical and root exudate indicators are correlated (Fig. S1b), we focused on five uncorrelated key predictors, including soil total N (N_j), P availability (PAV_j), soil moisture ($MOIST_j$), primary metabolite total soil sugars (TSS_j), and secondary metabolite glucosinolates (GLS_j), as well as the differential baseline ecological feature between natural forests and monoculture plantations (LU_j), i.e.

$$ORG_j = \vartheta_{0j} + \vartheta_{1j} LU_j + g_1(N_j) + g_2(PAV_j) + g_3(MOIST_j) + g_4(TSS_j) + g_5(GLS_j) \quad (5)$$

for $j \in$ {microbe abundance, fungi abundance, macrofauna abundance}.

Parameters ϑ_{0j} and ϑ_{1j}, and smoothing functions g_1, g_2, g_3, g_4, and g_5 were estimated from the GAM approach. By comparing the deviance of the full model and the reduced model that excluded the variable of interest, the contribution of each predictor variable in explaining variations in the soil organism indicators was estimated. Because soil moisture was highly correlated with pH (Pearson's $r = -0.878$; Fig. S1), the effect of soil moisture defined in Eqs. 3 and 5 also likely reflects the effect of pH.

3. Results

3.1. Soil physicochemical features associated with land management and plant physiology

Within the boundaries of oil palm, acacia, and eucalypt plantation concessions, the three forest set-aside areas had comparable soil physicochemical properties, including temperature, moisture content, litter thickness, N, P availability, SOC, and pH (Fig. 3; Table S1). This suggests that the baseline climate and environmental factors that may influence soil characteristics were similar throughout the three plantations. Soil total N, P availability, SOC, and pH were all naturally low (Fig. 3a-d), reflecting the soils present across the tropical region (Du et al., 2020). However, soil samples from the plantation sites exhibited significant difference in physicochemical properties from the forest set aside, which can be attributed to a variety of factors, including plantation management (such as planting density and the use of fertiliser and chemical input) and plant physiological traits.

Soil total N in oil palm plantations (OP_1, OP_2, and OP_3) and acacia plantations (AC_1, AC_2, and AC_3) was higher than in the adjacent forest (F_{OP} and F_{AC}), whereas soil N in eucalypt plantations (EU_1, EU_2, and EU_3) was similar to the forest area (F_{EU}) (Fig. 3a; Table 1). The differences in soil N between plantation types were most likely due to fertiliser application and plant physiology. In oil palm estates, a range of fertilisers are regularly added to compensate for natural infertility in soil and to enhance plant growth and fruit yield (Pardon et al., 2016; Skiba et al., 2020), Mineral fertilisers such as urea, organic fertilisers such as POME (palm oil mill effluent) and EFB (empty fruit bunches), and lime (calcium hydroxide) are examples of these (Comte et al., 2012). The application of high-N fertilisers explains the higher N content in soil under oil palm plantations compared to forests. Contrastingly, fertilisers are used sparingly in pulpwood plantations (Krisnawati et al., 2011; Hardiyanto et al., 2021), hence the soil total N here is expected to be the same as in forest area. However, leguminous species, such as acacia, can assimilate N from the atmosphere and enrich N content in soil (Wibisono et al., 2015), which may explain the greater N budget in acacia plantations compared to eucalypt plantations.

Soil P availability was much higher in oil palm plantations than forests, while P availability in acacia and eucalypt plantations was comparable to forest area (Fig. 3b; Table 1). Oil palm plantations intensively apply phosphatic fertilisers such as rock phosphate (RP), triple super phosphate (TSP), and diammonium phosphate (DAP)

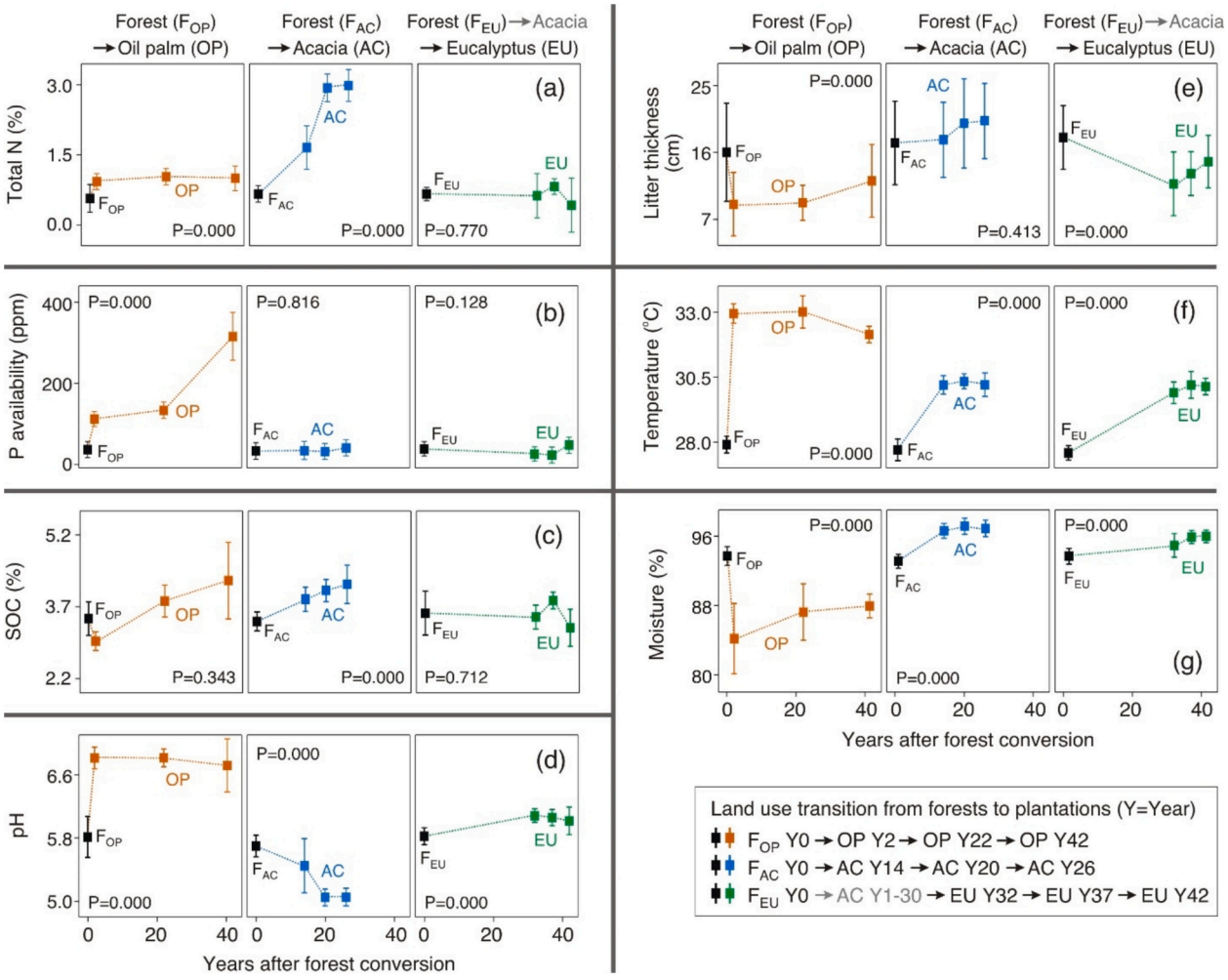

Fig. 3. Soil physicochemical properties in different land use transitions, including: (a) total N, (b) P availability, (c) soil organic carbon (SOC), (d) pH, (e) litter thickness, (f) temperature, and (g) moisture content. Land use transitions evaluated include: (i) the change from natural forests (at year 0) to oil palm plantations (year 2, 22 and 42 for new plantation, and second and third rotation, respectively), (ii) the change from natural forests (year 0) to acacia plantations (year 14, 20, and 26 for third, fourth, and fifth rotation), and (iii) the change from natural forests (year 0) to acacia plantations (year 1–30) then to eucalypt plantations (year 32, 37, and 42 for first, second, and third eucalypt rotation). Error bars represent 95 % confidence intervals. The numbers in each panel correspond to the *p*-values for significant differences between forests and plantations across multiple rotational periods (see Table 1). The statistical comparisons of soil properties across the three forest sites, representing baseline conditions, are provided in Table S1.

Table 1
The difference in soil physicochemical properties (N, P, SOC, pH, litter thickness, temperature, and moisture), plant root exudates (organic acids, total soil sugar, phenolic acids, allelochemicals, and glucosinolate), and soil organisms (microbes and soil macrofauna) between forest and plantations (combining multiple rotational phases), based on OLS regression outcomes with associated ANOVA tests. Plantations evaluated including oil palm (OP), acacia (AC), and eucalypt plantations (EU).

Soil aspect and variable	Plantation type	Plantation relative to forest		Mean value for		Significance	
		Estimate (95 % CI)		Plantations	Forest	*P*-value	‡
A. Soil physicochemical		Parameter α_1 in Eq. 1					
N	OP relative to F_{OP}	0.42	(0.30, 0.53)	1.00	0.58	0.000	●●●
	AC relative to F_{AC}	1.79	(1.41, 2.17)	2.47	0.67	0.000	●●●
	EU relative to F_{EU}	−0.04	(−0.31, 0.23)	0.63	0.67	0.770	ns
P	OP relative to F_{OP}	150.24	(93.11, 207.37)	188.66	38.42	0.000	●●●
	AC relative to F_{AC}	−0.83	(−7.97, 6.30)	34.14	34.98	0.816	ns
	EU relative to F_{EU}	−6.60	(−15.14, 1.95)	33.84	40.44	0.128	ns
SOC	OP relative to F_{OP}	0.23	(−0.25, 0.72)	3.69	3.46	0.343	ns
	AC relative to F_{AC}	0.59	(0.45, 0.73)	3.99	3.40	0.000	●●●
	EU relative to F_{EU}	−0.04	(−0.26, 0.18)	3.54	3.58	0.712	ns
pH	OP relative to F_{OP}	0.97	(0.84, 1.10)	6.79	5.82	0.000	●●●
	AC relative to F_{AC}	−0.51	(−0.67, −0.35)	5.19	5.70	0.000	●●●
	EU relative to F_{EU}	0.23	(0.17, 0.29)	6.06	5.83	0.000	●●●
Litter thickness	OP relative to F_{OP}	−5.88	(−8.60, −3.16)	10.22	16.10	0.000	●●●
	AC relative to F_{AC}	−1.55	(−5.32, 2.21)	16.65	18.20	0.413	ns
	EU relative to F_{EU}	−7.53	(−9.82, −5.25)	10.57	18.10	0.000	●●●
Temperature	OP relative to F_{OP}	4.80	(4.48, 5.13)	32.72	27.92	0.000	●●●
	AC relative to F_{AC}	2.55	(2.34, 2.77)	30.27	27.72	0.000	●●●
	EU relative to F_{EU}	2.50	(2.26, 2.74)	30.10	27.60	0.000	●●●
Moisture	OP relative to F_{OP}	−7.26	(−9.36, −5.16)	86.53	93.80	0.000	●●●
	AC relative to F_{AC}	2.77	(2.34, 3.20)	95.96	93.19	0.000	●●●
	EU relative to F_{EU}	1.92	(1.39, 2.45)	95.70	93.78	0.000	●●●
B. Plant root exudates		Parameter β_1 in Eq. 2					
Organic acids (OA)	OP relative to F_{OP}	175.86	(114.27, 237.45)	308.10	132.24	0.000	●●●
	AC relative to F_{AC}	344.90	(246.22, 443.58)	435.51	90.62	0.000	●●●
	EU relative to F_{EU}	127.48	(70.37, 184.58)	250.24	122.77	0.000	●●●
Total soil sugar (TSS)	OP relative to F_{OP}	−25.75	(−109.62, 58.12)	627.26	653.01	0.542	ns
	AC relative to F_{AC}	319.27	(171.34, 467.20)	954.99	635.73	0.000	●●●
	EU relative to F_{EU}	201.51	(137.25, 265.77)	693.03	491.52	0.000	●●●
Phenolic acids (PA)	OP relative to F_{OP}	20.37	(13.90, 26.84)	23.36	2.98	0.000	●●●
	AC relative to F_{AC}	162.05	(102.67, 221.43)	164.33	2.28	0.000	●●●
	EU relative to F_{EU}	138.88	(95.99, 181.76)	141.60	2.72	0.000	●●●
Allelochemicals (ALC)	OP relative to F_{OP}	1.53	(−2.26, 5.32)	4.87	3.34	0.423	ns
	AC relative to F_{AC}	76.71	(47.78, 105.63)	81.03	4.33	0.000	●●●
	EU relative to F_{EU}	56.53	(35.72, 77.34)	60.91	4.38	0.000	●●●
Glucosinolate (GLS)	OP relative to F_{OP}	−13.10	(−16.67, −9.54)	7.15	20.25	0.000	●●●
	AC relative to F_{AC}	−17.63	(−23.97, −11.29)	10.63	28.25	0.000	●●●
	EU relative to F_{EU}	−20.81	(−24.10, −17.52)	8.54	29.35	0.000	●●●
C. Soil organisms		Parameter δ_1 in Eq. 4					
Microbe abundance	OP relative to F_{OP}	17.33	(−60.71, 95.38)	165.03	147.70	0.659	ns
	AC relative to F_{AC}	−76.10	(−105.16, −47.04)	42.10	118.20	0.000	●●●
	EU relative to F_{EU}	−51.13	(−92.24, −10.02)	77.07	128.20	0.016	●
Fungi abundance	OP relative to F_{OP}	47.53	(17.93, 77.14)	75.33	27.80	0.002	●●
	AC relative to F_{AC}	148.93	(88.23, 209.64)	172.83	23.90	0.000	●●●
	EU relative to F_{EU}	30.83	(6.47, 55.20)	61.23	30.40	0.014	●
Fungi share of total microbes	OP relative to F_{OP}	0.41	(0.05, 0.76)	0.63	0.23	0.026	●
	AC relative to F_{AC}	5.86	(2.11, 9.61)	6.19	0.33	0.002	●●
	EU relative to F_{EU}	0.56	(0.21, 0.92)	0.84	0.28	0.002	●●
Soil macrofauna abundance	OP relative to F_{OP}	35.93	(−4.54, 76.40)	129.53	93.60	0.081	ns
	AC relative to F_{AC}	122.33	(48.23, 196.44)	255.23	132.90	0.002	●●
	EU relative to F_{EU}	142.07	(79.73, 204.40)	258.67	116.6	0.000	●●●

‡ ●●● *p*-value<0.001, ●● *p*-value<0.01, ● *p*-value<0.05, and ns with *p*-value>0.05.

(Comte et al., 2012), as well as lime (Mahmud and Chong, 2022), and all these can contribute to increased P availability in soil (Mkhonza et al., 2020; Kotowska et al., 2023). In contrast, fertiliser use is typically minimal in pulpwood plantations, which could explain why acacia and eucalypt plantations had similar levels of P availability as forests. Acacia plantations had greater SOC level than forests, whereas oil palm and eucalypt plantations had levels that were comparable to those of forests (Fig. 3c; Table 1). The higher amount of SOC in acacia plantation was most likely due to the plant's ability to fix atmospheric nitrogen, which increased soil fertility and organic carbon (Zhang et al., 2018). While soil pH in oil palm plantations was found to be significantly higher than in forest, soil pH in eucalypt plantations was similar to the forest area, and soil pH in acacia plantations was significantly lower than forests (Fig. 3d; Table 1). Lime application could be attributed to inflated soil pH in oil palm plantations (Mohammed et al., 2014; Mahmud and Chong, 2022), whereas soil acidification in acacia plantations was most likely linked to the plant's physiology as an N-fixer (Sawada et al., 2021).

Out of the three plantations we evaluated, eucalypt plantations had the thinnest litter layer, followed by oil palm plantations, while acacia plantations had the thickest layer, comparable to forests. (Fig. 3e; Table 1). The GAM analysis of the data across the three plantations suggests that litter thickness had a positive correlation with soil N, but negative correlation with P availability (albeit marginally) (Fig. S2a).

The high soil total N in the acacia plantations - the highest of the three planting types (Fig. 3a) - may be responsible for the tick litter layer, as this hinders the decomposition of the acacia litter. The eucalyptus plantations' thinner litter layer compared to oil palm plantations can be attributed to the former's higher soil N (Fig. 3a).

When compared to the nearby forests, the temperature of the soil on oil palm plantations was noticeably higher (Fig. 3f, Table 1). Soil temperature in acacia and eucalypt plantations was greater than in forests but lower than in oil palm plantations of similar age (Fig. 3f; Table 1). Oil palm plantations' higher soil temperature compared to forests was most likely caused by forest removal and sparse planting. Oil palm trees are normally spaced 7–10 m apart to allow for growth. Although the crown width of two-year-old oil palm trees can reach 6 m, certain areas between young plants remain unshaded (Tao et al., 2016; Gérard et al., 2017). Because of this portion of the ground being exposed to direct sunlight, soil temperature was unsurprisingly high in young oil palm plantations (Meijide et al., 2018; Romero et al., 2022). In addition, litter layers beneath soil under oil palm plantations were thin to buffer against high ground temperatures (Fig. 3e). Unlike oil palm plantations, acacia or eucalypt trees for the pulpwood estate are normally planted 2–3 m apart, and after two years these trees can reach a height of 6–8 m with a crown width of 1.5 m, reducing canopy gaps between trees (Hegde et al., 2013). This canopy closure may have reduced soil exposure to solar heat, resulting in more moderate soil temperature. Across plantation sites, we found that soil moisture was positively correlated with litter thickness (albeit marginally) but negatively correlated with temperature (Fig. S2b).

3.2. Root exudates following changes in soil physicochemical features

The concentration of primary metabolite OA in root exudates were significantly higher under oil palm, acacia, and eucalypt plantations compared to forests adjacent to the respective plantations (Fig. 4a; Table 1). Primary metabolite TSS exudates were significantly higher under acacia and eucalypt plantations compared to forest, but oil palm plantations had similar TSS as forest area (Fig. 4b; Table 1). OA and TSS compounds increased progressively over successive plantation rotations in both oil palm and acacia plantations. The concentration of OA and TSS exudates was primarily related to P availability (accounting for >39 % of the total variation in the data), followed by total N and soil moisture (Fig. 5a-b). These two exudate compounds were only slightly impacted by the ecological differences between monoculture plantations and natural forests. The level of OA and TSS increased with increasing P availability and soil moisture. Both compounds decreased as soil N increased, but increased with excess N (i.e., both compounds were lowest at moderate N). High total N in soil and soil moisture in acacia plantations was likely contributing to elevated OA and TSS in root exudates (Fig. 3a, g), and elevated moisture content in soil could play a key role in increasing both exudate compounds in eucalypt plantations (Fig. 3g).

The concentration of secondary metabolite PA in root exudates were significantly higher under oil palm, acacia, and eucalypt plantations compared to forests within proximity to the respective plantations (Fig. 4c; Table 1). ALC were also significantly higher under acacia and eucalypt plantations compared to forests, but oil palm plantations had similar ALC as forest area (Fig. 4d; Table 1). The concentration of PA and

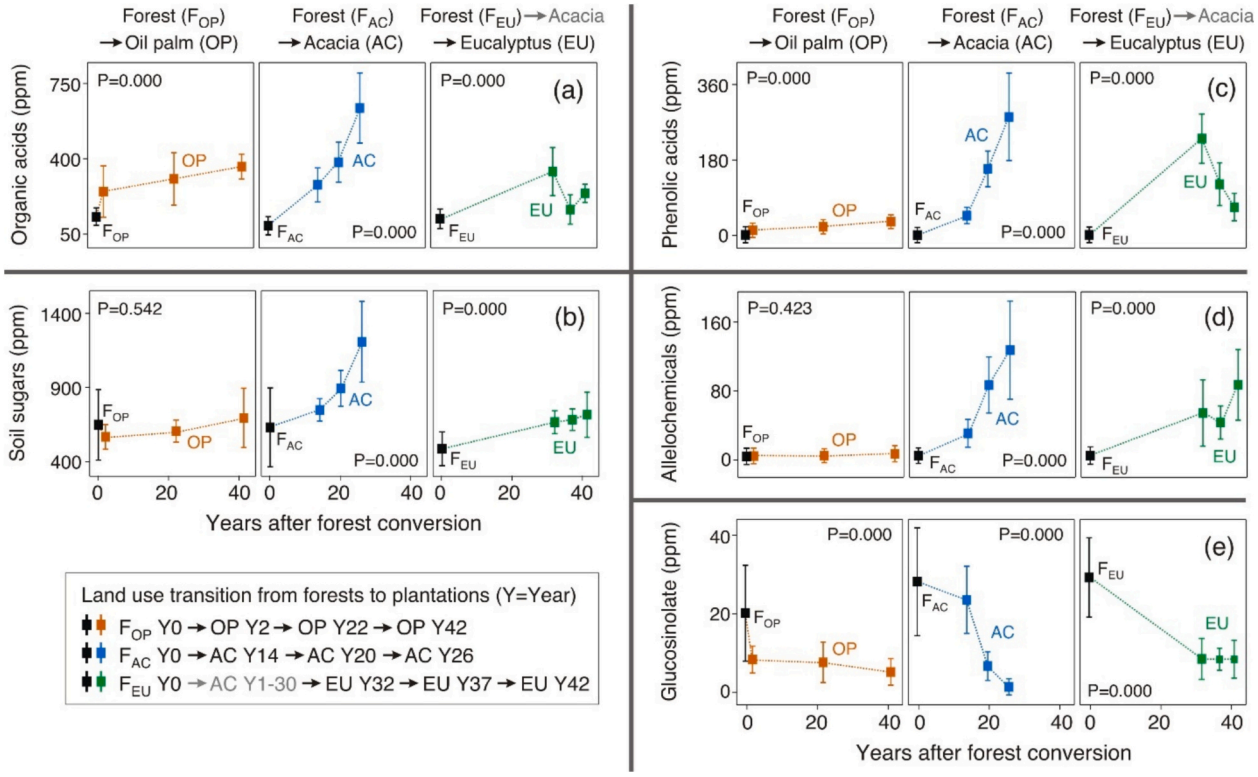

Fig. 4. Plant root exudates in different land use transitions, including primary metabolite exudates (a) organic acids (OA) and (b) total soil sugars (TSS), and secondary metabolites (c) phenolic acids (PA), (d) allelochemicals (total of terpenes, alkaloids, phenols) (ALC), and (e) glucosinolates (GLS). Land use transitions evaluated include: (i) the change from natural forests (at year 0) to oil palm plantations (year 2, 22 and 42 for new plantation, and second and third rotation, respectively), (ii) the change from natural forests (year 0) to acacia plantations (year 14, 20, and 26 for third, fourth, and fifth rotation), and (iii) the change from natural forests (year 0) to acacia plantations (year 1–30) then to eucalypt plantations (year 32, 37, and 42 for first, second, and third eucalypt rotation). Error bars represent 95 % confidence intervals. Numbers in each panel correspond to the p-value representing significant differences between forests and plantations, aggregated across various rotational periods (see Table 1). Additional significant tests comparing forest soil conditions at the three sites, representing baseline conditions, are provided in Table S1.

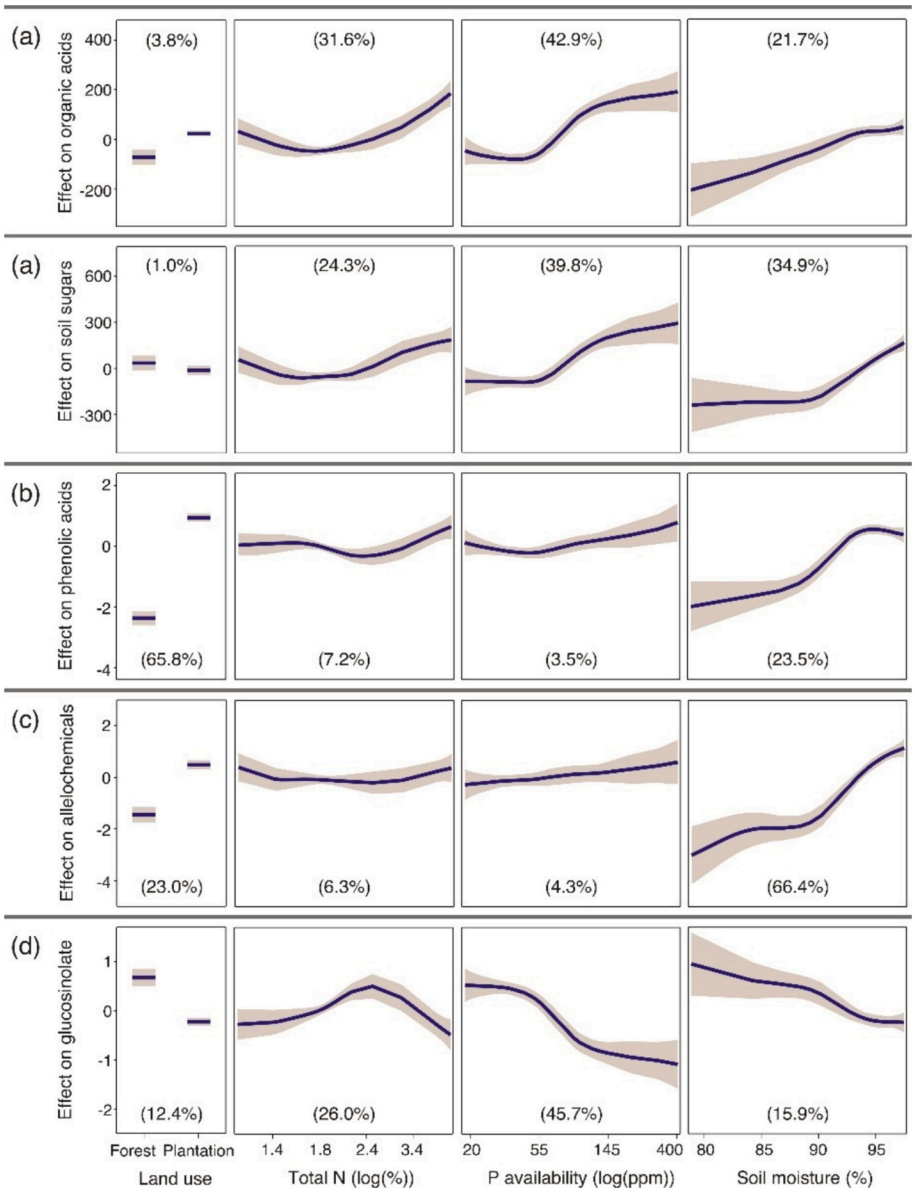

Fig. 5. The effect of soil physicochemical properties such as total N, P availability, and soil moisture and difference in baseline ecological properties of natural forest versus monoculture plantations on plant root exudates, including primary metabolite exudates (a) organic acids (OA) and (b) total soil sugars (TSS), and secondary metabolites (c) phenolic acids (PA), (d) allelochemicals (total of terpenes, alkaloids, phenols) (ALC), and (e) glucosinolates (GLS). Number inside the parenthesis within each panel indicates the relative contribution of each predictor variable in explaining variation in the response variable. The data were fitted using the semi-parametric GAM approach. The Pearson correlation coefficient between the fitted value derived from the GAM and the actual data is 0.866 for OA (a), 0.817 for TSS (b), 0.936 for PA (c), 0.871 for ALC (d), and 0.820 for GLS (e), suggesting superior model fits. Blue lines indicate the trends, while shaded regions indicate the 95 % confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ALC was primarily correlated with soil moisture and the differential ecological feature between natural forests and monoculture systems (Fig. 5c-d). This contrasts the pattern observed for the primary metabolites OA and TSS whereby the differential ecological property between natural forest and monoculture was only marginal (Fig. 5a-b). Furthermore, increased levels of PA and ALC were linked to increased soil moisture. The presence of low levels of PA and ALC compounds in oil palm plantations compared to moderate levels in acacia and eucalypt trees was consistently correlated with high soil moisture levels in these trees and low soil moisture levels in oil palm plantations (Fig. 3g).

The concentration of secondary metabolite GLS in root exudates were significantly lower in all plantations evaluated compared to forests (Fig. 4e). Over successive plantation rotations, this exudate compound decreased progressively. The GLS level was strongly correlated with P availability (accounting for 45.7 % of the total variation in the data), total N (26.0 %), and soil moisture (15.9 %) (Fig. 5e). GLS levels increased in response to decreased P availability and soil moisture. GLS levels also increased with rising soil N content but fell with excess N (rendering it optimal at moderate soil N). The low GLS concentration in oil palm plantations could be attributed to the elevated P availability rising progressively through the plantation rotations (Fig. 3b). High soil moisture likely played an important role in reducing GLS levels in acacia and eucalypt plantations (Fig. 3g). Excess N in soil might also further contribute to GLS metabolite reduction in acacia plantations (Fig. 3a).

3.3. Soil organisms associated with soil physicochemical characteristics and root exudates

The abundance of soil microbe was significantly lower under acacia and eucalypt plantations compared to forests, but under oil palm plantations microbe abundance was the same as in forest area (Fig. 6a). Soil microbe abundance in eucalypt plantations was lower than in forests but higher than in acacia plantations. Microbe abundance was largely correlated with P availability in soils (30.3 % of the total variation in the data) and total N content (26.4 %), and moderately with TSS in root exudates (15.5 %) (Fig. 7a). The increase in microbe abundance in soil was associated with increased P availability but reduced total N and TSS exudate. In acacia and eucalypt plantations, higher TSS was most likely associated with a reduction in microbial abundance. Increased N in soil could have further reduced microbes in acacia plantations.

The abundance of fungus in soil was significantly higher for all three plantations evaluated compared to forest area (Fig. 6b). Moreover, the fungal share of total microbes was markedly elevated in the plantation soils (Fig. 6c). Among the plantations, acacia sites exhibited the highest fungal abundance, substantially surpassing levels observed in both oil palm and eucalypt plantations (Fig. 6b-c). Based on the GAM analysis, fungal abundance in soils is strongly related to soil physicochemical properties, with soil moisture having the greatest effect (accounting for 28.6 % of the total variation in the data), along with total N (24.5 %) and P availability (20.4 %) (Fig. 7b). As soil moisture has a strong negative correlation with soil pH (Fig. S1), the strong effect of moisture likely also reflects the effect of pH. The concentration of GLS in root exudates also accounted for 16.8 % of the overall variation in the data. Fungal abundance increased with increasing soil moisture, P availability, and GLS concentration. Fungi responded non-linearly to total N in soils, with fungal abundance lowest at moderate soil N content. The high abundance of fungus in acacia plantations appeared to be related to increasing total N and soil moisture (which correlates with increasing soil acidity). Increasing soil moisture (which correlates with more acidic environments) was linked to increased fungal abundance in eucalypt plantations, and increasing P availability was associated with increased fungal abundance in oil palm plantations.

The abundance of soil macrofauna was markedly higher under acacia and eucalypt plantations compared to natural forests, but macrofauna abundance was the same between oil palm plantations and forests (Fig. 6c). The abundance of soil macrofauna appears to be attributed largely to soil moisture (which accounted for 41.8 % of the total variation in the data), total N (21.5 %), and the ecological differences between natural forests and monoculture systems (16.4 %) (Fig. 7c). GLS and TSS exudates from roots had very little effect on soil macrofauna, which contrast to the results found in microbes and fungi alone. The abundance of soil macrofauna increased with increasing soil moisture but decreasing total N. Increased soil moisture appeared to play a significant role in the abundance of soil macrofauna in acacia and eucalypt plantations (Fig. 3g).

4. Discussion

The conversion of natural forests to monoculture plantations can have a significant impact on soil ecosystems through various interconnected pathways, including direct and indirect effects on soil physicochemical properties, plant root exudates, and soil organism assemblage. These mechanisms can be influenced by both external (e.g. plantation management practice) and internal factors (e.g. plant physiological characteristics). Findings show that soil physicochemical characteristics varied significantly across land uses, reflecting the direct effects of different plantation regimes, particularly planting density and the use of fertilisers and chemicals, as well as plant physiology, particularly the ability of leguminous species such as acacia to assimilate N

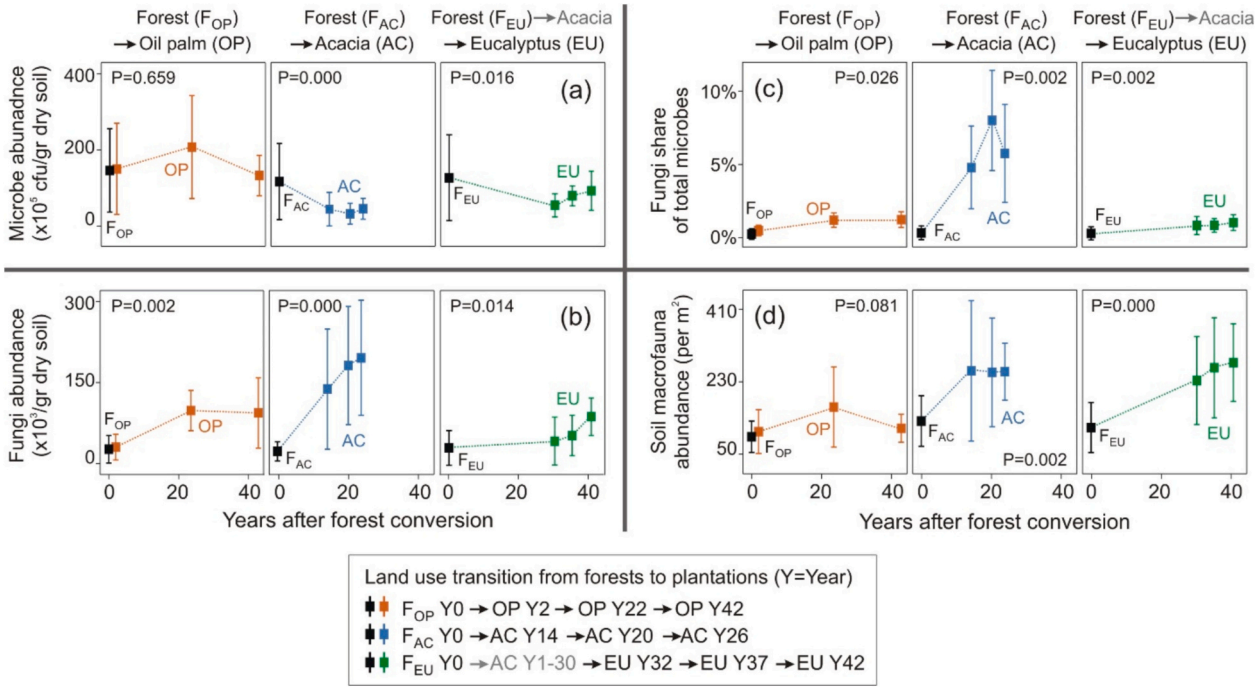

Fig. 6. Soil organisms in different land use transitions, including: (a) the overall abundance of microbes (bacteria, fungi, and actinomycetes), (b) abundance of fungi alone, (c) fungi share of total microbes, and (d) abundance of soil macrofauna (nematodes, annelids, and arthropods). Land use transitions evaluated include: (i) the change from natural forests (at year 0) to oil palm plantations (year 2, 22 and 42 for new plantation, and second and third rotation, respectively), (ii) the change from natural forests (year 0) to acacia plantations (year 14, 20, and 26 for third, fourth, and fifth rotation), and (iii) the change from natural forests (year 0) to acacia plantations (year 1–30) then to eucalypt plantations (year 32, 37, and 42 for first, second, and third eucalypt rotation). Error bars represent 95 % confidence intervals. Numbers in each panel represent *p*-values indicating significant differences between forests and plantations, combining data from multiple rotation periods (see Table 1). Detailed results for differences between forest sites at the baseline (year 0) are provided in Table S1.

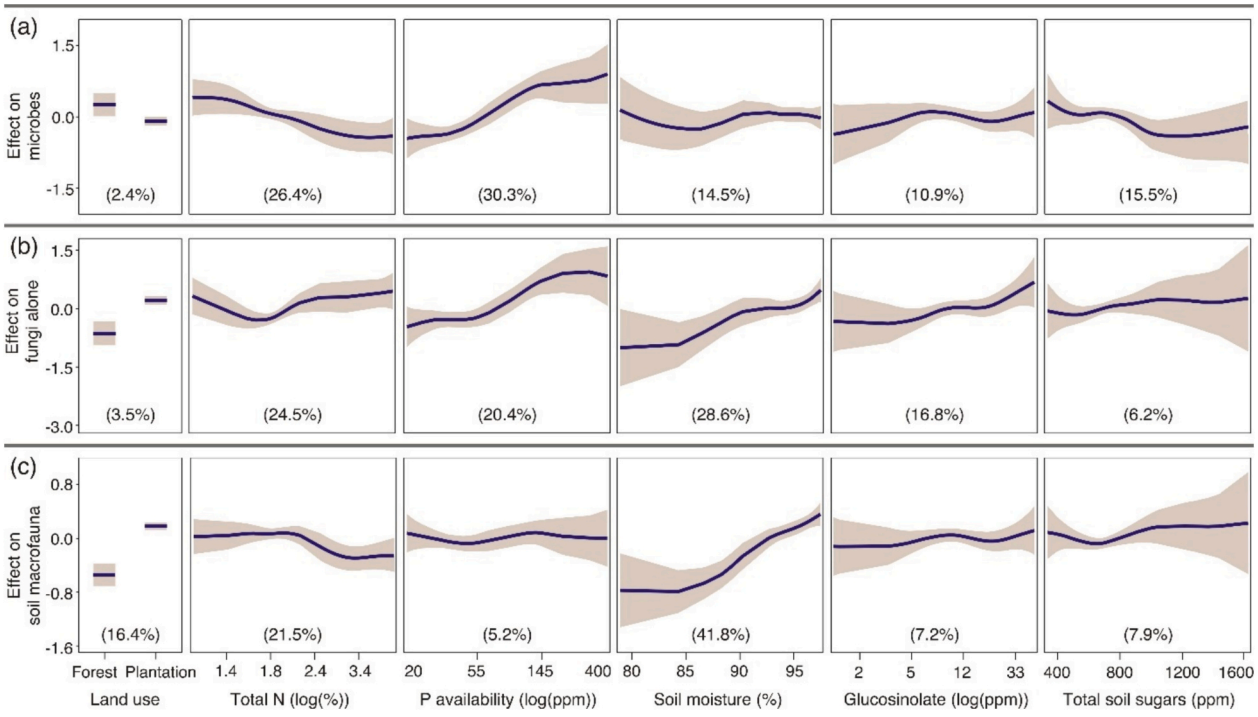

Fig. 7. The effect of soil physicochemical properties (total N, P availability, and soil moisture), differential baseline ecological properties between natural forest and monoculture plantations, and root exudates (glucosinolates (GLS) and soil sugars (TSS)) on soil organisms, including: (a) microbes (bacteria, fungi, and actinomycetes), (b) fungi alone, and (c) soil macrofauna (nematodes, annelids and arthropods). The number inside the parenthesis within each panel indicates the relative contribution of each predictor variable in explaining variation in the response. The data were fitted using the semi-parametric GAM approach. The Pearson correlation between the fitted value estimated from the GAM and the actual data is 0.733 for microbes (a), 0.752 for fungus alone (b), and 0.748 for macrofauna (c), indicating good model fits. The trends are indicated by the black lines, while the shaded regions reflect the 95 % confidence range.

from air and accumulate it in soils. Trees in pulpwood plantations are typically planted at a much higher density than in oil palm plantations (Tao et al., 2016; Gérard et al., 2017). Dense pulpwood tree planting could promote vertical growth and higher biomass per unit area. On the other hand, oil palm trees are sparsely planted to allow for their larger size and the need for sunlight to reach the lower parts of the plant. To sustain optimal productivity in fruit production, oil palm plantations rely on substantial and regular applications of fertilisers and chemicals (Dubos et al., 2017; Darras et al., 2019), whereas pulpwood plantations typically apply minimal fertiliser (Krisnawati et al., 2011; Hardiyanto et al., 2021).

Our findings across monoculture plantations show that soil nutrients and plant physiological capacity in nutrient cycling affect root exudates differently in different plantations. A moderate increase in OA and TSS concentrations in oil palm plantations were associated with increased P availability, which was also correlated with increased soil pH from lime application (Mahmud and Chong, 2022) and increased soil organic carbon from organic fertiliser input (POME and EFB) (Comte et al., 2012). Sufficient P levels in oil palm plantations may promote plant growth and, as a result, increase TSS release into the rhizosphere (Carvalhais et al., 2011). Because of increased microbial activity and organic matter decomposition, high soil organic carbon can contribute to higher levels of OA (Wu et al., 2009; Hau et al., 2020). An increase in OA and TSS in both acacia and eucalyptus plantations were primarily associated with increased soil moisture. Acacia plantations benefit from increased N due to the plant's ability to fix nitrogen, which amplifies the effect of OA and TSS in the rhizosphere. Higher soil moisture and water availability in pulpwood plantations foster microbial activity in the rhizosphere, resulting in increased OA secretion (Hasegawa et al., 2023). TSS production is a byproduct of increased photosynthesis and metabolic activity in plants, which can be enhanced by increased soil moisture (Hasegawa et al., 2023).

Abiotic (physical processes) and biotic (interaction with other species) factors can both cause a plant to release root exudate compounds, and the significance of these factors can vary depending on the metabolite, most notably between primary metabolites responsible for plant functioning and growth and secondary metabolites responsible for plant's interaction with other species. Natural forests allow for much richer interactions between different species than monoculture systems (Marjakangas et al., 2020; Filgueiras et al., 2021), so reduced diversity in monoculture can be expected to have a greater impact on secondary metabolite production than primary metabolite production. After controlling for external factors in various land uses, such as land management and plant physiological traits, our study demonstrates that, for the primary metabolites AO and TSS, the differences in ecological properties or diversity between natural forests and monocultures were found to be a negligible factor (Fig. 5a-b). In this case, differential ecological properties contributed to only 3.8 % and 1 % of variations in AO and TSS, respectively. This was not the case, however, for secondary metabolites, whereby the differences in ecological properties between forests and monocultures is a strong determinant, particularly for the allelopathic compounds PA and ALC (i.e., ecological characteristics explained 65.8 %, 23 %, and 12.4 % of the variations in PA, ALC, and GLS, respectively) (Fig. 5c-e). Therefore, ecological diversity is critical for secondary metabolite development but less important for primary metabolite production. These results also indicate that, although the primary metabolites that drive plant growth can be physically modified by applying suitable land management techniques considering plant's physiological traits (Canarini et al., 2019; Bornø et al., 2022), the secondary metabolites that control the plant's defence and competitive strategy most likely evolve through much more complex mechanisms influenced by physical processes as well as interaction, feedback, and adaptation with other species (Kessler and Kalske, 2018; Weinhold et al., 2022).

While we found that secondary metabolites involved in the plant's interaction with other species, including GLS, to be significantly lower in all three plantations when compared to natural forests, PA and ALC were

found to be higher in plantations, particularly in acacia and eucalypt monocultures. PA and ALC are important components of the plant-plant interface, particularly in competition, allelopathy, and inhibiting the growth of other plants (Macías et al., 2007). These compounds have been discovered in greater abundance in range-expanding plants than in native species (González-Teuber et al., 2017). Numerous studies have suggested that the accumulation of PA and ALC in soil is one of the key factors limiting continuous monocropping of exotic plants by causing self-toxicity (Zhao et al., 2021; Ullah et al., 2023). GLS, on the other hand, is a secondary metabolite involved in herbivore and pathogen defence (Singh, 2017). Plants produce this metabolite in response to environmental stressors such as nutrient and water availability (Petretto et al., 2019; Shawon et al., 2020). Plants' long-term response and adaptation to water availability in their native environment has also been shown to shape GLS production, with plants originated or evolved in arid and semi-arid savanna or nutrient-scarce environments having lower GLS concentrations than those evolved in wetter regions, presumably due to lower enemy pressure or limited resource availability in the former (Tomiolo et al., 2017; Metz and Tielbörger, 2023). Acacia and eucalypt are native to the savanna biome of Australia and Africa, but they have spread globally with tree reintroduction initiatives (Sanchez et al., 2018; Hutapea et al., 2023). These trees' natural habitat may determine the presumably lower baseline GLS production compared to humid tropical forest. Increased water availability (soil moisture) can further reduce GLS levels because plants reduce their investment in defence-purpose metabolites in response to abundant nutrients (Omirou et al., 2013; Tong et al., 2014), explaining the low concentration of GLS observed in acacia plantations. Similarly, abundant nutrients from fertiliser inputs may account for the low GLS concentrations observed in oil palm plantations (Pant et al., 2015; Sharma et al., 2023).

Our analysis further shows that the abundance of fungi in all three plantations studied were higher than in forest areas, despite a lower overall microbial abundance. This disparity results in a notably elevated proportion of fungi in the soil microbial within plantations. Coupled with plantations' lower defensive capacity, evidenced by reduced levels of secondary metabolite GLS, which have not had the opportunity to develop and evolve due to a lack of interaction with other species and high nutrient input, renders these plantation soil environments more susceptible to disease (Mohammed et al., 2014). Among the three plantations, acacia had the highest level of fungal organisms, making it highly prone to diseases (Hegde et al., 2013; Mohd Farid et al., 2022). More research is required to determine the duration of monoculture's presence that could have long-term repercussions on soil health. Nonetheless, our findings underscore the importance of enhanced diversity in monoculture environments for effective disease suppression in plants and soil ecosystems.

Our study is subject to several limitations, which also highlight promising directions for future research. The plate counting method used to assess microbial activity has inherent constraints, as it only detects microorganisms that can grow on specific media, thereby excluding many unculturable species. We chose this method primarily because our focus was on diverse indicators of soil functioning and health, rather than solely on microbial diversity. Future research could employ molecular techniques, such as high-throughput sequencing, for a more comprehensive analysis of microbial communities and a deeper understanding of how soil microorganisms vary across different land-use types. Additionally, although we explored the relationships between soil, roots, and organisms under different land-use patterns, we did not dissect the direct and indirect impacts of land-use change and management practices. Future studies could benefit from more complex statistical approaches, such as structural equation modelling (SEM), to investigate these interactions more thoroughly.

5. Implications for land use policy

While monoculture plantation systems are recognised for their significant detrimental effects on tropical environment, the discussion usually centres on how these systems displaced natural forests. Prior to 2017, Indonesia's oil palm plantation sectors reflected this issues, as massive forest conversion to oil palm plantations occurred during this period (Gaveau et al., 2022). With the recent slowdown in oil palm expansion, focus has shifted to the sector's biodiversity performance and ability to lessen reliance on intensive agricultural chemical inputs. (Darras et al., 2019; Lam et al., 2019). In recent years, there has been a call for greater diversification in oil palm monoculture to address these issues, such as through agroforestry and intercropping with diverse native trees (Khasanah et al., 2020; Purwanto et al., 2020; Zemp et al., 2023). Enriching plant diversity is currently mandated by the Indonesian government to be used in oil palm plantations, particularly those developed on state forest land, as there are up to 3.4 million hectares of illegal oil palm plantations occupying state forests (Astuti et al., 2022). While sanctioning this "*keterlanjuran*" or oversight is deemed problematic (Astuti et al., 2022), the national government proposed a new policy called "*jangka benah*" or corrective measure that requires the simultaneous planting of a set of native trees in oil palm plantations until the plantation rotation is completed and the land can be returned to forests through natural regrowth (Peteru and Komarudin, 2022).

Even when fertilisers and herbicides are restricted, monoculture systems of alien trees may negatively impact the ecosystem by decreasing soil health. Our findings show that acacia and eucalyptus monocultures were associated with soil toxicity and increased prevalence of fungal in soil, and such a long-term scheme can eventually threaten the health of the broader ecosystem (Wang et al., 2022; Faucon et al., 2023). Although it has long been suggested that combining different tree species in plantation forestry can boost stand-level productivity by allowing for complementary resource uses (Paula et al., 2020; Feng et al., 2022), more recent arguments have reinforced the necessity of combining exotic and different native trees in plantations in tropical environments to enhance resilience (Amazonas et al., 2018; Wang et al., 2019). Plantation forestry is anticipated to expand in the future across tropical regions in response to growing incentives for carbon offsetting projects to achieve net zero emissions globally (Cooper and MacFarlane, 2023; Nofyanza et al., 2023). Mixed-species plantations with native trees, thus, ought to be promoted, if not mandated.

CRediT authorship contribution statement

Enny Widyati: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sadino:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Sugeng Budiharta:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Acep Akbar:** Writing – review & editing, Investigation. **Adi Susilo:** Writing – review & editing, Investigation. **Agus Kurniawan:** Writing – original draft, Investigation. **Asep Sadili:** Writing – review & editing, Investigation. **Diana Prameswari:** Writing – review & editing, Investigation. **Edi Mirmanto:** Writing – review & editing, Investigation. **Etik Erna Wati Hadi:** Writing – review & editing, Investigation. **Mustaid Siregar:** Writing – review & editing, Investigation. **Marfuah Wardani:** Writing – review & editing, Investigation. **Naning Yuniarti:** Writing – review & editing, Investigation. **Nina Mindawati:** Writing – review & editing, Investigation. **Parlin H.P. Pasaribu:** Writing – review & editing, Investigation. **Ragil S.B. Irianto:** Writing – review & editing, Investigation. **Ratri Ma'rifatun Nisaa':** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Sri Een Hartatik:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Sri Suharti:** Writing – review & editing, Investigation. **Sutiyono:** Writing – review & editing, Investigation. **Titi Kalima:** Writing – review & editing, Investigation. **Ulfah Karmila Sari:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Wida Darwiati:** Writing – review & editing, Investigation. **Wieke**

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106253.

Data availability

Data will be made available on request.

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