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Soil organic carbon recovery in tropical tree plantations may depend on restoration of soil microbial composition and function

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ABSTRACT

Soil organic carbon (SOC) supports essential functions in terrestrial biomes and global biogeochemical cycles, and tropical tree plantations are often called upon to reverse deforestation-induced SOC loss. Yet the comparative efficacy of different plantation types and associated drivers of SOC restoration remain unclear. Theory suggests that higher chemical and spatial heterogeneity of plant litter should promote greater efficiency of soil microbial communities involved in SOC formation, so we hypothesised that more species-diverse tree plantations should be more effective in accelerating recovery of SOC. To test this, we compared developmental recovery of SOC and soil microbial communities between monoculture (*Swietenia macrophylla* King, mahogany) and highly diverse and mostly native species plantations (termed "rainforestation"). All plantation types, which were aged 15 to 20 years, only restored the composition of the soil microbial community to 20–30% of the reference, selectively logged old-growth rainforest. Contrary to our hypothesis, mahogany plantations, but not rainforestation, restored SOC and microbial function. Rainforestation shifted soil microbial composition and the composition of the understory vegetation closer to reference conditions. Soil microbial composition at all plantation sites was correlated with plant composition and functional traits, and better explained variation in SOC than land use. In particular, soil fungal PLFA biomass displayed a strong positive correlation with topsoil SOC concentration. This suggests that belowground restoration with tropical reforestation is slow relative to typical rotation times of tropical plantations (15–20 years). We conclude that reliable and rapid restoration of SOC may depend on interventions both above and below ground to re-instate the soil microbial community. This may require careful selection of plant species in combination with microbial inoculations.

1. Introduction

Ecosystem services such as carbon sequestration, flood mitigation and nutrient retention depend critically upon soil organic matter. Soil organic matter, largely composed of soil organic carbon (SOC), is crucial in highly-weathered tropical soils, conferring much of their physical, chemical and biological properties (Feller and Beare, 1997). In weathered tropical soils with limited presence of active clay minerals, SOC fortifies most of the physical and chemical soil characteristics beneficial to plant growth, including pH modulation and cation/anion exchange, water- and nutrient-holding capacities (Lal, 2016; Smith et al., 1999). Land-clearing and soil disturbance typically catalyse SOC loss through decomposition and erosion (Post and Kwon, 2000), which begets carbon emissions to the atmosphere, nutrient leaching, loss of soil physical, chemical and biological functions, in turn limiting plant growth and net primary productivity, with follow-on effects of degraded landscapes such as flood exacerbation (Bruijnzeel, 2004; Smith et al., 1999). Returning SOC to degraded tropical landscapes is integral to restoring soil function, ecosystem productivity, and associated ecosystem services. Reversal of degradation stemming from land-clearing

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would intuitively be accomplished through forest restoration, but results to date present no clear pattern of efficacy in the short term (Marín-Spiotta and Sharma, 2013).

Characterisation of the soil microbial community may present an early means to quantify the trajectory and effectiveness of forest restoration for recovering SOC (Shao et al., 2019a). While soil microbes are the principal agents of SOC decomposition, they also seem to be a dominant source of SOC (Cotrufo et al., 2013; Grandy and Neff, 2008; Kallenbach et al., 2016; Miltner et al., 2012, 2009). A likely constraint on SOC formation potential is the efficiency with which soil microbes incorporate plant matter into their biomass, metabolites and exudates (Cotrufo et al., 2013). While labile substrate can be used more efficiently on chemical grounds (Cotrufo et al., 2013), evidence is emerging that chemically complex plant residues promote microbial communities that are more efficient at converting substrate into biomass (Amin et al., 2014; Bonner et al., 2018; Fanin and Bertrand, 2016). In addition, it appears that soil fungi, which tend to be associated with complex substrate (De Boer et al., 2005; McGuire and Treseder, 2010) contribute more to SOC formation than bacteria (Jastrow et al., 2007; Li et al., 2015; Malik et al., 2016; Six et al., 2006). Studies in agroecosystems generally find higher SOC levels to be associated with fungi-dominated microbial communities (Six et al., 2006). Soil fungi seem critical for the physical protection of soil C, as soil aggregation and aggregate stability appear to be predominantly mediated by fungi (Bossuyt et al., 2001; Caesar-tonthat, 2002). Another potentially integral role of fungi for SOC generation is that fungal necromass may in part be more resistant to decomposition than bacterial necromass (Guggenberger et al., 1999; Holland and Coleman, 1987; Li et al., 2015; Malik et al., 2016; Rillig et al., 2007; Six et al., 2006). In particular, soil fungi synthesise extremely stable proteins and melanins, both of which bear strong chemical resemblance with components of stable SOC (Knicker, 2011; Paim and Linhares, 1990). Taken together, the above suggests that SOC increases when plant residues (i) provide an abundance of high-quality substrate that can be efficiently metabolised into microbial biomass, and (ii) are sufficiently heterogeneous chemically and spatially to promote an efficient and fungi-dominated microbial community. Heterogeneity is likely to benefit competitiveness of fungi because their typically mycelial growth form and broad enzymatic spectrum is advantageous for homogenising resources and for accessing enzymatically intractable and physically obscured substrate (De Boer et al., 2005; Guhr et al., 2015; Strickland and Rousk, 2010).

According to this theoretical framework, increased chemical and spatial heterogeneity of plant residues under higher diversity tree plantings ought to benefit SOC recovery by means of promoting efficient, fungi-dominated microbial communities. Indeed, some mixed plantings or secondary forests outperform monocultures for SOC restoration (Behera and Sahani, 2003; Li et al., 2005; Sang et al., 2012; Wang et al., 2017), but the mechanisms – which may include chemical, thermal, or microbial effects – have yet to be explicitly examined, and empirical studies of microbial community traits under tropical plantations of contrasting floristic compositions are rare.

In this study, we examined the responses of soil microbial communities and SOC to the early decades of establishment of monoculture plantations and high-diversity mixed-species plantations in the Philippines, addressing in particular the paucity of empirical data on soil microbial restoration. We hypothesised that the reforestation examined in this study will increase SOC levels, with this change reflected in early increases in the soil fungal-to-bacterial biomass ratio, and that mixed-species plantations will bring about greater recovery of SOC and soil microbial function and composition than monocultures.

2. Methods

2.1. Site description

The study was performed on tree plantations located in the central-western region of Leyte Island in the Philippines. Leyte lies at the eastern side of the central Philippines, within the Eastern Visayas region, spanning the north latitudes 9°55′ and 10°48′ and east longitudes 124°17′ and 125°18′. The island has an equatorial climate, with means during the 1980–2000 period of annual temperatures at sea level ranging from 26 °C to 29 °C and mean annual precipitation between 2700 and 4000 mm (Nguyen et al., 2012) (there is trend in the Philippines of 0.1 °C warming per decade over the period 1951–2010). A brief dry season occurs from March to May. Leyte Island is traversed from north to south by a geologically young mountain range running atop the Philippines Fault Line. The major soil geologies of central-western Leyte are basalt and limestone, giving rise to the Maasin clay (Typic Paleudults) and Lugo clay (Typic Eutrudepts) soil types (Carating et al., 2014) with mean pH in our samples of 5.1 ± 0.1 and 5.9 ± 0.3 respectively.

2.2. Study design

We evaluated a site network composed of two reference conditions (10 sites in coconut-grassland mixed land use – the baseline prior to plantation establishment – and 5 sites in selectively logged native forest – the target for restoration) and two plantation types (5 sites in monoculture plantations 15–20 years old and 5 sites in high diversity mixed-species plantings 17–19 years old) (Fig. 1; Table S1). The monoculture plantations (hereafter “mahogany”) were planted with *Swietenia macrophylla* King (Meliaceae), and the high-diversity mixed-species plantations (hereafter “rainforestation”) were planted with various combinations from a seedling pool of *circa* 100 species, most of them native, including Dipterocarpaceae trees (Nguyen et al., 2016, 2012). These plantations are unlikely to have experienced much active management (Herbohn et al., 2014). Species composition and management of the rainforestation plots are described in more detail by Nguyen et al. (2016, 2014). As reference for planting intervention, the plantations were sampled alongside pairwise matched grassland sites with sparse coconut palm (*Cocos nucifera* L., Arecaceae) overstory, each situated within 100 m of their plantation counterpart and with similar aspect and slope. The adjacent grasslands are typical of the sites on which the plantations would have been established. While the precise management of these grassland sites is unknown, typically there would have been little active management and it is unlikely that any substantial amounts of fertilizer would have been applied. As a reference for well-developed forest with minimal soil disturbance, sites located in regenerating selectively logged native rainforest with no recent history of clear-felling were sampled. All sites were between 0.1 and 1 ha in area. Two mahogany plantation sites were situated on limestone-derived soils (Lugo clay, a.k.a. Typic Eutrudepts), all others were on basalt substrates (Maasin clay, a.k.a. Typic Paleudults). In total, 25 sites were sampled, distributed across 15 locations spanning approximately 100 km from north to south, each at least 2 km from its nearest neighbour, with sufficient interspersion among plantation types to mitigate spatial autocorrelation effects (Wills et al., 2017).

2.3. Understory plant community

For a subset of our sites (4 of 5 sites for each of mahogany and rainforestation plantations and all 5 reference forest sites), understory plant traits were assessed as part of a previous study described in full by Wills et al. (2017), using methods based on those established by Herbohn et al. (2014). Briefly, two to four circular plots were established per site, with a five metre radius (78 m^2) extending from the centre point. Position and number of plots per site varied depending on forest size and shape, in order to prevent edge effects. All plants less than two metres in height were included in the assessment. Plants were identified to species level by local botanists from Visayas State University.

Continuous measures of functional traits including specific leaf area (cm^2/g), leaf nitrogen concentrations (LNC, % dry leaf mass) and leaf

Fig. 1. The four land uses in eastern Philippines examined in this study: (a) mahogany monoculture plantation, (b) "rainforestation" mixed species plantation, (c) coconut-grassland land use adjacent to plantations, and (d) regenerating selectively logged rainforest.

phosphorus concentrations (LPC, % dry leaf mass), were collected following standard protocols (Pérez-Harguindeguy et al., 2013). LNC and LPC were determined using a single digestion method, which used a colorimetric determination of LNC, using the salicylate-hypochlorite method (Baethgen and Alley, 1989), and LPC using an adaptation of a single solution method (Anderson and Ingram, 1989) used by Murphy and Riley (1962). Discrete traits including dispersal type (animal, wind, water, gravity propulsion, or multiple types), fruit type (achene, berry, capsule, drupe, follicle, legume, nutlet, samara, cone or syncarp), fruit size and seed size were determined based on species identity as described by Wills et al. (2017). Fruit and seed sizes were coded, with fruit size dimensions of **1** = " < 2 mm × < 2 mm", **2** = "2–5 mm × 2–5 mm", **3** = "6–15 mm × 6–15 mm", **4** = "16–25 mm × 16–25 mm", **5** = "26–100 mm × 26–100 mm", **6** = " > 100 mm in any dimension"; and seed size dimensions of **1** = "0–1 mm × 0–1 mm", **2** = "1.1–3 mm × 1.1–3 mm", **3** = "4–8 mm × 4–8 mm", **4** = "9–12 mm × 9–12 mm", **5** = " > 13 mm in any dimension".

2.4. Soil sampling

Soils were collected over three weeks in April of 2015. In each site (land use type), plots were established with the goal of maximizing the sampled area without incurring edge effects of neighboring land uses. Nine sampling points were then measured to include a central point, four edge points halfway between the central point and plot borders along lines parallel and orthogonal to the slope, and four points pairwise equidistant between the edge points. Topsoil cores to 10 cm depth were collected at all nine points to be pooled for microbial analyses. Soil samples were collected with a hand auger at 0–10 cm, 20–30 cm and 40–50 cm depth from the central location and four edge points for chemical analyses.

2.5. Soil chemical analysis

The total organic carbon (C) of soils sampled from all depths in each site was quantified at the ACIAR analytical laboratory at Visayas State University in the Philippines using Heane's method (Heanes, 1984). Total nitrogen (N) and phosphorus (P) were determined by digesting soil samples with Kjeldahl digestions, where concentrations of N in digests were quantified following the method described by Baethgen and Alley (1989), and P concentrations were determined using the method described by Murphy and Riley (1962). Soil pH was determined potentiometrically with water as dilutant using a pH meter.

2.6. Soil microbial analysis

The abovementioned nine topsoil samples (0–10 cm) from each plot were pooled into a bulked sample, which was then subsampled five times for subsequent incubation. These samples were kept field-moist for one week to ameliorate confounding effects of labile C (Brackin et al., 2013) before acclimation in soil microcosms for six days under standardised conditions at 27 °C, 80% humidity and 60% water holding capacity. This involved placing 40–45 g unsieved soil into microcosms constructed out of 50 mL centrifuge tubes (Inselsbacher et al., 2009) followed by incubation in the dark. All subsequent microbial analyses were performed on these acclimated soils. This procedure was used to minimise dissimilarity in environmental conditions between land uses (*e.g.* plantations and adjacent grassland soils may experience vastly different microclimate at a given point in time) in order to capture differences in baseline microbial characteristics.

Respiration was measured thrice over three days in five microcosms for each land use replicate using similar methods as described by Bonner et al. (2018). For two hours the microcosms were sealed with rubber stoppers (Brackin et al., 2013) with cresol red (Rowell, 1995) in 1% agar gel (Campbell et al., 2003) inside. The cresol red gel, which changes colour with the pH change induced by CO_2 absorption (Rowell, 1995), was set in individual microtitre plate wells that were affixed to the inside walls of the microcosms with reusable adhesive. To quantify CO_2 concentration, the absorbance of the cresol red wells at 590 nm was read using a plate reader (Spectramax Plus 384, Molecular Devices, San Francisco, CA, USA).

After respiration had been measured, the microcosm soil was passed through a 2 mm hand sieve to facilitate enzyme activity assays, catabolic profiling and phospholipid fatty acids (PLFA) analysis. The fluorescein diacetate (FDA) assay was used to estimate total enzyme activity in four soil microcosms for each land use replicate (FDA is a colourless model substrate hydrolysed by most hydrolytic enzymes into the coloured compound fluorescein) (Adam and Duncan, 2001).

Enzyme efficiency, a metric of microbial efficiency calculated in a variety of ways previously (Fanin and Bertrand, 2016; Sinsabaugh et al., 2002; Wickings et al., 2012), was estimated here as the quotient of total enzyme activity and mean respiration.

The MicroResp system, described by Campbell et al. (2003), was used for catabolic profiling of the soil microbial community. The correspondence between this type of catabolic profile and microbial function at a broader scale is unclear, but this method nonetheless tends to successfully differentiate contrasting soils (Romaniuk et al., 2011). Briefly, deep-well microplates were filled with *circa* 300 mg per well of sieved soil, pooled from the harvested microcosms. Fifteen organic substrates dissolved in distilled water (keeping the amount of C and water consistent between substrates) and a distilled water control were then added to three wells each, making for three technical replicates. Soil CO_2 efflux in response to the added substrates over 12 h was estimated colourimetrically with cresol red as described above. Three sugars (glucose, fructose, sucrose), two carboxylic acids (citric acid, malic acid), two phenolic acids (vanillic acid, syringic acid), six amino acids (phenylalanine, tryptophan, arginine, glutamine, glycine, lysine), an amino sugar (glucosamine) and phytic acid dipotassium salt were used. These compounds are biologically relevant and capture a range of chemical complexity and nutrient content. Respiration responses to substrates were adjusted by subtracting values obtained from only water addition, and then scaled by the sum of all responses for the sample to account for differential baseline respiration (Leff et al., 2012). We calculated Shannon's diversity index, to characterise catabolic 'entropy' as a metric of catabolic diversity, using the equation $E = -\Sigma_i p_i \ln p_i$, where p_i is the respiration induced by the *i*:th substrate expressed as a proportion of the sum of all respiration rates.

On three subsamples from the bulked soil harvested from microcosms, PLFA analysis was used to assess soil microbial composition, using a protocol described by Bossio and Scow (1998). Very briefly, the protocol relies on lipid extraction from lyophilised soil with chloroform:methanol:phosphate buffer, separation of phospholipids with solid phase extraction columns, and then analysis with a gas chromatograph. We favoured PLFA analysis over genomic methods as quantitative characterisation of relative biomass of groups was prioritised over fine taxonomic resolution. Fatty acids thought to be of bacterial origin (i15:0, a15:0, 15:0, i16:0, 16:1ω7, i17:0, a17:0, cy17:0, 17:0, 18:1ω7 and cy19:0) were summed to estimate an index of bacterial biomass, and 18:2ω6,9 provided an index of fungal biomass (Frostegard and Baath, 1996). The fatty acids i15:0, a15:0, i16:0, i17:0 and a17:0 provided an index of gram positive bacterial biomass, and 16:1ω7, 18:1ω7, cy17:0 and cy19:0 were used for gram negative biomass (Wilkinson et al., 2002). All microbial PLFAs were summed as an index of microbial biomass (Joergensen and Wichern, 2008).

2.7. Statistics

As land use was replicated five times, the number of treatment replicates for all analyses was five. All analyses were performed using R, version 3.2.4 (http://www.r-project.org/), with the packages 'lme4', 'ggplot2', 'multcomp', 'lsmeans', 'MuMIn', 'lavaan', and 'vegan' (Barton, 2016; Bates et al., 2015; Hothorn et al., 2008; Lenth, 2016; Oksanen et al., 2016; Rosseel, 2012; Wickham, 2009).

Model fitting and testing was performed using PERMANOVA ('adonis' in 'vegan'), generalised (Gamma-distributed log-link) and Gaussian linear mixed-effects models, and Tukey's Honest Significance test. All candidate models for SOC were ranked computationally based on AICc (corrected Akaike Information Criterion) with the 'dredge' function in 'MuMIn'. Models were tested for heteroscedasticity, non-normality and outlier leverage.

The matrices representing soil microbial function (MicroResp responses, FDA enzyme activity and mean respiration) and composition (PLFA values) were ordinated into 15 orthogonal axes, then compared with the Procrustes superimposition permutation test with 9999 permutations, which is a stronger alternative to the Mantel test for assessing multivariate correlations (Guillot and Rousset, 2013; Lisboa et al., 2014; Peres-Neto and Jackson, 2001). The choice of ordination for orthogonal projection of microbial characteristics was PCA (principal components analysis) after Chord transformation. Chord distance appropriately addressed large differences in vector magnitudes (such as between fungal and bacterial PLFAs) liable to obscure directional differences, and yielded the best explanatory power to constraining variables in distance-based RDA performed on this dataset when compared with Hellinger or χ^2 distances (Legendre and Gallagher, 2001). Hellinger-transformed PCA (the distance metric was chosen as above) of the matrices of plant species composition (species counts) and plant functional composition (SLA, LNC, LPC, counts of plants with each type of dispersal method, fruit type, seed and fruit size classes) allowed Procrustes tests with 9999 permutations in 15 dimensions of correlations between aboveground and belowground composition and function. Two dimensional non-metric Multidimensional Scaling (NMDS) using Chord distance facilitated visualisation of land use effects on soil microbial function and composition, as this method more effectively collapsed variance into two dimensions than PCA, but these axes were less appropriate for matrix operations (such as Procrustes and permutation tests) due to their non-metric nature. Plant taxonomic and functional composition were visualised with NMDS using Hellinger distance. Distance-based RDA (Chord) with MicroResp data, enzyme activity and respiration as response and as constraining axes the first four principal components from Chord-transformed PCA on PLFA data, followed by permutational significance test (9999 permutations) provided a means to corroborate the Procrustes test for correlation between soil microbial composition and function. Similarly, Chord-transformed data used in partial RDA ordinations, with 'soil geology' (basalt or limestone) and 'site' as conditioning variables, which provide a means to partial out variation akin to random effects in a mixed model, followed by permutation tests with 9999 permutations allowed evaluation of statistical significance of land use effects on microbial composition and function.

Variance partitioning was used for estimating relative explanatory power of microbial function and composition (each represented by a matrix of the first three principal components from the abovementioned PCA, representing ~90% variation in each), and land use on soil organic C. Similarly, structural equation modelling ('sem' in 'lavaan') partitioned 'direct' and 'indirect' effects of land use on SOC. Only models with at most nine parameters (with 75 observations available for many variables) could reliably be fitted, so this analysis was applied as an adjunct to computational model selection, using variables already found important in this prior analysis. Robust maximum likelihood estimation of standard errors and test statistics with Satorra-Bentler scaling (Rosseel, 2012) was used to address violation of multivariate normality. Structural equation models were excluded if the robust Comparative Fit Index fell below 0.95 and robust Root Mean Square Error of Approximation surpassed 0.05.

3. Results

3.1. Soil organic matter

A generalised linear mixed effects model partitioning out background variation across sites and soil geologies revealed that land use had a significant effect on mean SOC over all three sampled depths extending to 50 cm ($P < 0.001$). Regenerating selectively logged forests had the highest mean SOC at 3.4 [2.3, 5.0] % (mean with asymmetric confidence interval, representing stand error range back-transformed from log scale), which was significantly higher than rainforestation plantations at 1.3 [0.9, 1.9] % but not mahogany plantations at 2.5 [1.9, 3.4] % (Fig. 2). Only mahogany brought about a significant increase in SOC compared with its baseline grassland reference land use, but the baseline did not significantly differ from the

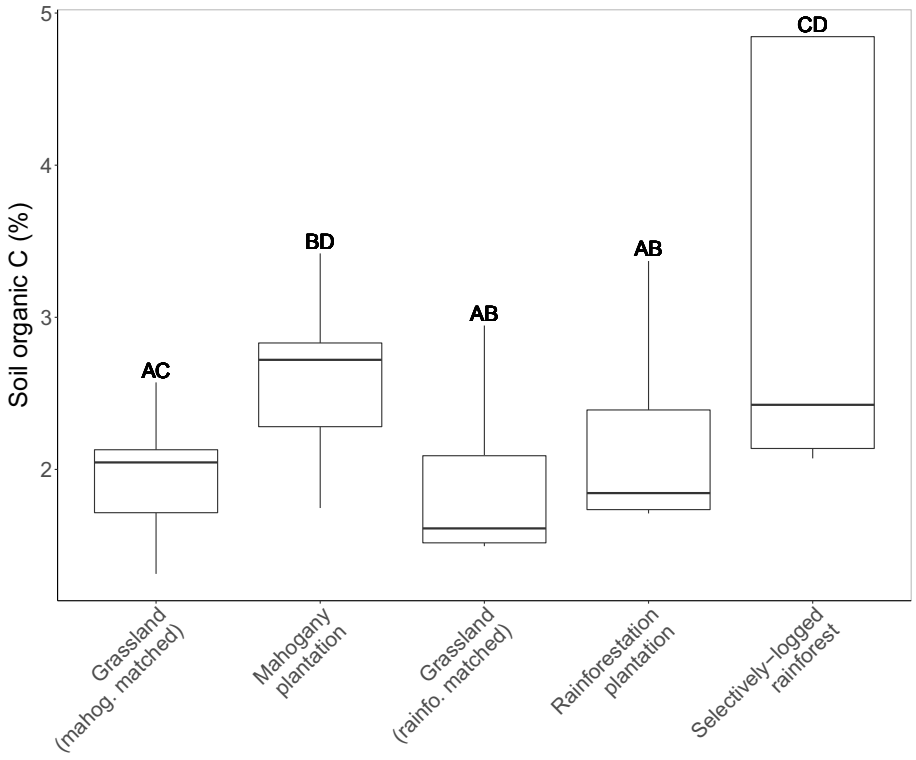

Fig. 2. Soil organic C concentrations in the top 50 cm of soil, predicted (adjusted for random background variation) by a Gamma-distributed generalised linear mixed effects models where 'soil geology' (basalt or limestone) and 'site' are random grouping variables, under two types of plantation and their adjacent reference grassland-coconut land use (representing baseline land use prior to plantation establishment), as well as regenerating, selectively logged native forest with no recent history of clear-felling, on Leyte Island, Philippines. Mahogany plantations were established as monocultures of *Swietenia macrophylla*, "rainforestation plantations" were established as high-diversity mixtures. Letters are from Tukey pairwise comparisons (distinct letters indicate distinct means).

Table 1
Raw means and standard errors of chemical characteristics of the top 50 cm of soil and dry weight of standing leaf litter stock under five tropical land uses in the Philippines. Letters in superscript are derived from Tukey post-hoc comparisons from mixed effects models (with soil geology and site as random grouping variables), and distinct letters within a row indicate distinct means.

	Mahogany-matched grassland	Mahogany plantation	Rainforestation-matched grassland	Rainforestation plantation	Selectively-logged rainforest
C/N ratio	15.0 ± 2.3^{A}	15.5 ± 2.3^{A}	12.0 ± 1.1^{A}	11.5 ± 1.0^{A}	14.4 ± 1.6^{A}
Total N (%)	0.16 ± 0.02^{AC}	0.22 ± 0.03^{BD}	0.18 ± 0.02^{AB}	0.22 ± 0.02^{AB}	0.25 ± 0.04^{CD}
Total P (‰)	0.69 ± 0.1^{A}	0.80 ± 0.1^{A}	0.65 ± 0.1^{A}	0.64 ± 0.1^{A}	0.59 ± 0.1^{A}
pH	5.6 ± 0.3^{AB}	5.7 ± 0.3^{AB}	5.0 ± 0.1^{A}	5.0 ± 0.1^{A}	5.3 ± 0.1^{B}
Litter (g DW m^{-2})	32.4 ± 5.5^{AB}	523.3 ± 76.6^{CD}	67.3 ± 16.5^{A}	208.9 ± 31.6^{BC}	400.8 ± 50.1^{D}

selectively logged forest, which was not true of rainforestation baseline soils (Fig. 2). Soil N exhibited the same pattern across land uses as SOC, with lowest values in rainforestation and its paired baseline grassland sites, highest in selectively logged forests, and an increase with mahogany planting (Table 1). Soil pH displayed a similar pattern, but did not increase significantly with mahogany planting, and C/N ratio and total soil P did not differ significantly with land use (Table 1). Standing leaf litter was significantly increased in both types of plantation compared with their paired grassland reference sites (approximately ten- and four-fold in mahogany and rainforestation, respectively), and did not significantly differ between plantation land uses, but reference rainforest standing litter was significantly higher than in rainforestation (Table 1).

Relative importance of land use *versus* metrics of microbial composition and function (such as enzyme efficiency and the ratio of fungal biomass to bacterial biomass) as predictors for SOC were compared by computationally ranking linear mixed effects models. The optimal model out of these varied with depth (Table 2). The optimal model for topsoil SOC (0–10 cm) included only fungal biomass ($P < 0.001$) and gram-positive to gram-negative bacterial biomass ratio ($P < 0.01$) with positive and negative coefficients respectively. SOC concentrations at greater depths (20–30 cm and 40–50 cm) as well as mean SOC concentration down to 50 cm were best predicted solely by land use ($P < 0.001$). At all depths, standing litter stock was the poorest predictor of SOC, although it was a statistically significant predictor when included alone. Regenerating selectively logged forest accounted for much of the land use effect, so when the same analysis was performed on the subset of data with this land use removed, fungal biomass was the best predictor of SOC overall and at 40–50 cm depth, and no predictor improved on the null model (only intercept) for SOC at 20–30 cm depth, indicating that error was overpowering statistical power. Structural equation modelling suggested that a substantial part of land use effects on SOC to 50 cm may be indirect, perhaps occurring, among other avenues, *via* changes in fungal biomass and gram-positive to gram-negative bacterial biomass ratio (Fig. 3). Similarly, variance partitioning indicated that only 0.65% of the variance in SOC was uniquely explained by land use independently of soil microbial composition and function (the remainder of the variance explained by land use, 12.3%, was shared by microbial composition or function), and microbial composition explained more variation in SOC than land use (Fig. S1).

Topsoil pH and mean SOC to 50 cm were strongly correlated, but fungal biomass was not significantly correlated with pH when background variation across sites and soil geologies was accounted for, indicating that fungal biomass variation across land uses was not simply a result of pH variation in turn resulting from SOC variation.

3.2. Belowground and aboveground biotic recovery

Permutation tests on partial redundancy analysis (conditioned on soil geology and site) with Chord-transformed data indicated that land

Table 2
Rankings of importance of top five univariate predictors for SOC (soil organic C) at each depth, from AICc (corrected Akaike Information Criterion) comparisons of all linear mixed-effects models with all combinations of ten possible predictors (the six listed in the table and four not in the top five at any depth: total microbial biomass, gram-positive bacterial biomass, microbial enzyme efficiency and standing leaf litter stock). 'Soil geology' (basalt or limestone) and 'site' were included as random grouping variables in all models. 'Akaike weight' of a predictor is calculated from the number of models in which it is included and their AICc weights. 'Correlation' refers to the sign and significance of correlation between predictors and response from a Pearson's product-moment test, and the rightmost column shows which predictors were included in the best of all models for that response.

SOC depth	Predictor	Akaike weight	Correlation	In best model?
0–10 cm	Fungal biomass	0.76	+***	Yes
	Gram-positive: gram-negative bacterial biomass	0.53	−***	Yes
	Shannon's catabolic diversity	0.43	+	No
	Gram-negative bacterial biomass	0.35	+***	No
	Land use	0.33	Factor***	No
20–30 cm	Land use	1.00	Factor***	Yes
	Shannon's catabolic diversity	0.43	–	No
	Gram-positive: gram-negative bacterial biomass	0.41	−***	No
	Fungal biomass	0.37	+***	No
	Fungal: bacterial biomass	0.11	−	No
40–50 cm	Land use	0.98	Factor***	Yes
	Shannon's catabolic diversity	0.45	−	No
	Fungal biomass	0.41	+***	No
	Gram-positive: gram-negative bacterial biomass	0.36	−**	No
	Fungal: bacterial biomass	0.10	+*	No
Mean 0–50 cm	Land use	1.00	Factor***	Yes
	Fungal biomass	0.37	+***	No
	Shannon's catabolic diversity	0.36	–	No
	Gram-positive: gram-negative bacterial biomass	0.26	−***	No
	Fungal: bacterial biomass	0.09	+	No

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

use was a significant predictor of soil microbial function and composition ($P = 0.001$ for both), a result corroborated by PERMANOVA using the same distance metric. Both plantation types brought about minor shifts in soil microbial function and composition towards those of regenerating selectively logged forest (Fig. 4), which was largely functionally and compositionally distinct from the other land uses. Specifically, soil microbial composition was not convergent on reference communities in either plantation type, but rainforestation soil communities scattered closer to reference communities in microbial compositional space (Fig. 4a), with the two best predictors of SOC, fungal biomass and bacterial gram ratio, tracking towards reference rainforest levels with reforestation. In contrast, soil microbial function under mahogany plantations appeared convergent on regenerating selectively logged forests while that under rainforestation plantations was not (Fig. 4b). A Procrustes superimposition permutation test indicated that soil microbial function and composition were significantly correlated ($P < 0.001$), which was corroborated by Chord-transformed redundancy analysis, where 48% of the variance in microbial function was explained by microbial composition.

Taxonomic composition of understory vegetation was not recovered

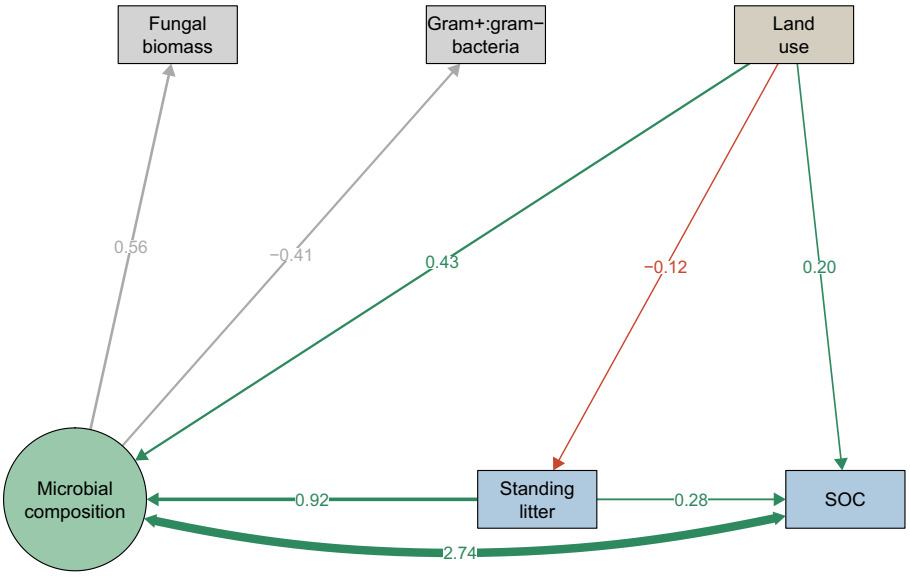

Fig. 3. Path diagram of a structural equation model characterising direct and indirect effects of differential land use – monoculture and mixed plantations and their respective baseline grassland states, as well as selectively logged rainforest – on soil organic carbon (SOC) concentration in the top 50 cm. 'Microbial composition' is a latent variable defined by soil fungal biomass and the biomass ratio of gram-positive to gram-negative bacteria (both assessed using PLFA analysis), the two strongest microbial correlates of SOC in this dataset. The inclusion of such a latent variable is to better represent the hypothesised underlying connections: land use has an effect on traits of microbial composition that correlate with SOC, and fungal biomass and bacterial gram ratio are indicators of these traits. 'Standing litter' was measured as standing stock of leaf litter. Thickness of connecting lines is proportionate to the standardised effect size of correlation between nodes, depicted also by the printed numbers within each arrow. For example, the model indicates a direct land use effect size on SOC of 0.2, compared with a (maximal) potential effect *via* microbial recomposition of 0.43. Because land use is a categorical factor, the sign (±) of the effect size on other variables is without meaning, whereas the negative sign for the contribution of gram ratio to microbial composition tells us *inter alia* that there is a negative correlation between SOC and gram ratio ($-0.41 \times 2.74 < 0$). A two-way arrow between SOC and microbial composition represents potential for each to influence the other, as well as potential existence of unmeasured third factors driving both in parallel.

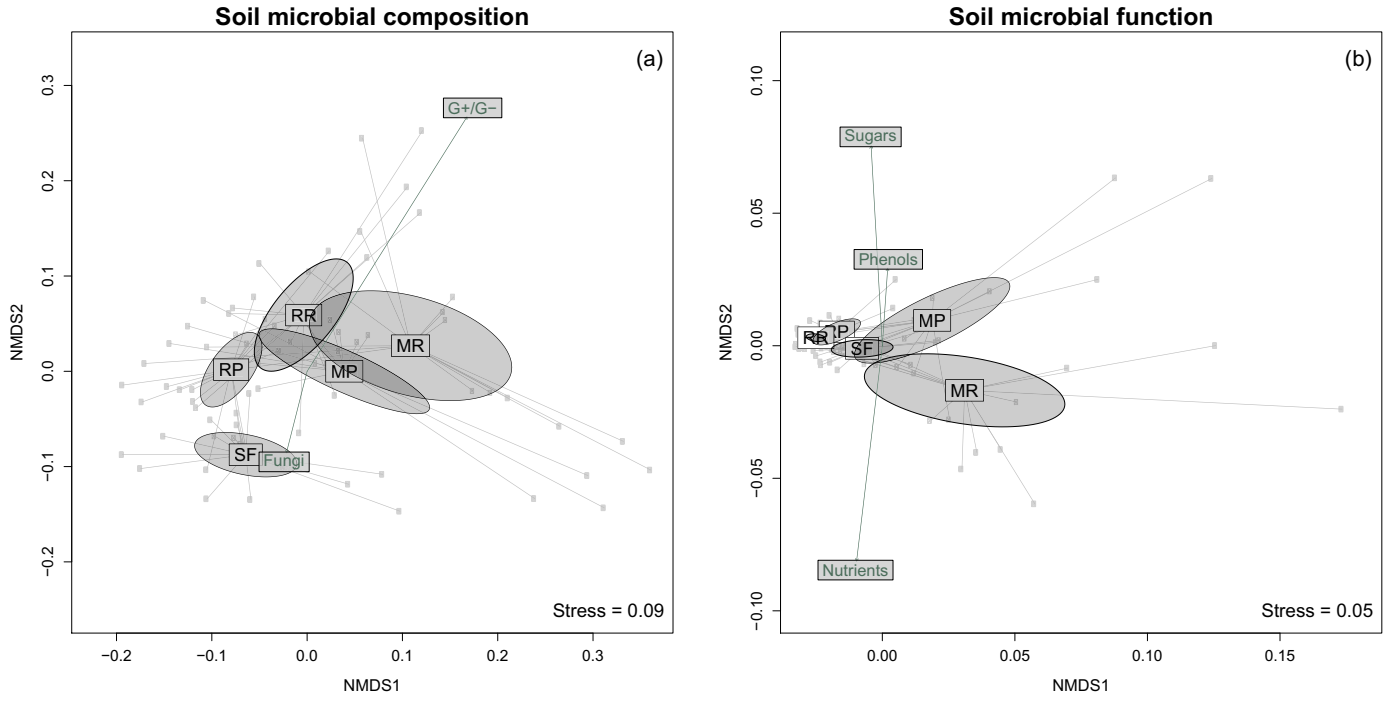

Fig. 4. Two-dimensional non-metric multidimensional scaling (NMDS) output depicting land use differences in (a) soil microbial composition assessed by PLFA analysis and (b) soil microbial function assessed through substrate use, enzyme activity and respiration. The land uses represented are located on Leyte Island in the Philippines; 'MP' and 'MR' correspond to mahogany (*Swietenia macrophylla*) monoculture plantations and adjacent grassland-coconut reference land uses (the baseline prior to plantation establishment) respectively, 'RP' and 'RR' correspond to rainforestation plantations and adjacent grassland reference sites, and 'SF' corresponds to regenerating selectively logged forest. 'G + /G-' and 'Fungi' represent directions of increase of gram-positive to gram-negative bacterial biomass ratio and fungal biomass, while 'Sugars', 'Phenols', and 'Nutrients' represents directions of increase in responses to compounds of these types; nutrients are amino acids and an amino sugar (glucosamine). Chord distance was used for both ordinations, and ellipses represent 95% confidence intervals. A Procrustes superimposition permutation test indicated that microbial composition and function were strongly correlated ($P < 0.001$).

in either type of plantation (Fig. 5a), and plant functional composition was recovered in rainforestation but not mahogany plantations (Fig. 5b). All four pairings of soil microbial composition and function *versus* understory plant taxonomic composition and functional compositions were significantly correlated ($P \leq 0.001$ for all, Table 3).

4. Discussion

The scale of deforestation and subsequent establishment of tree plantations is especially vast in the tropics (Keenan et al., 2015), and expanding human populations and poverty make restoration of tropical forest ecosystems particularly pressing (Kettle, 2012). There is a need to understand SOC trajectories of tropical plantations, which requires considerably more empirical data than is currently available. We examined the responses of soil microbes and SOC to contrasting types of tropical plantation, mahogany monoculture and high diversity rainforestation. These plantations were juxtaposed against reference grassland-coconut baseline sites, which represent land use prior to plantation establishment, and regenerating selectively logged rainforest reference sites, which represent the comparatively undisturbed soil conditions prior to forest clearing. Soil organic C increased significantly with mahogany but not rainforestation planting, although there was an indication (not statistically significant) that the mahogany plantations were established on more fertile sites with higher baseline SOC (based on the statistical overlap between mahogany baseline soils and selectively logged rainforest, not shared by rainforestation baseline soils). This caveat hinders conclusive insight about the relative speed of SOC restoration with either form of planting. The results do not support our hypothesis that higher diversity plantations perform better than monocultures with respect to SOC restoration. Also contrary to our hypothesis, our analysis suggests that mahogany plantations recovered soil microbial function and mixed-species rainforestation plantations did not. Conversely, and in line with our hypothesis, soil microbial composition was further on the path to recovery under rainforestation than mahogany plantings. Taken together, the results indicate that full soil microbial recovery does not occur under the studied plantation types within the timeframes commonly focused in tropical forestry, where plantation rotation lengths often range from 10 to 20 years.

The best model for SOC varied with soil depth, with characteristics of microbial composition the best predictors for topsoil organic C, and land use the best predictor for subsoil organic C. Differences in SOC between selectively logged rainforest and the other land uses studied were particularly pronounced in the subsoil. This accounts for the strong correlation between land use overall and SOC below 20 cm; land use was no longer the best predictor of SOC at any depth with selectively logged rainforest removed from analysis, indicating this land use accounts for most of the land use effect. With no recent history of clear-felling and agricultural use, these reference rainforest sites are demonstrating a pattern of slower SOC decline with depth compared with more disturbed sites, seen previously (Li and Mathews, 2010; Skjemstad et al., 1999).

The ratio of gram-positive: gram-negative bacterial biomass was correlated negatively with SOC at all depths. This result is at odds with observations that i) microbial residues contribute substantially to SOC (Kallenbach et al., 2016), potentially to the extent that microbial biomass can predict future increases in SOC (Shao et al., 2019a), and ii) gram-positive bacterial residues have substantially higher stability than gram-negative residues (Schmidt et al., 2011). On the other hand, our result may reflect a difference in substrate preference, with certain gram negative bacteria potentially proliferating on a more robust supply of labile C in high SOC soils (Fanin et al., 2019). The limited taxonomic resolution of PLFA analysis is drawn into focus here, as we

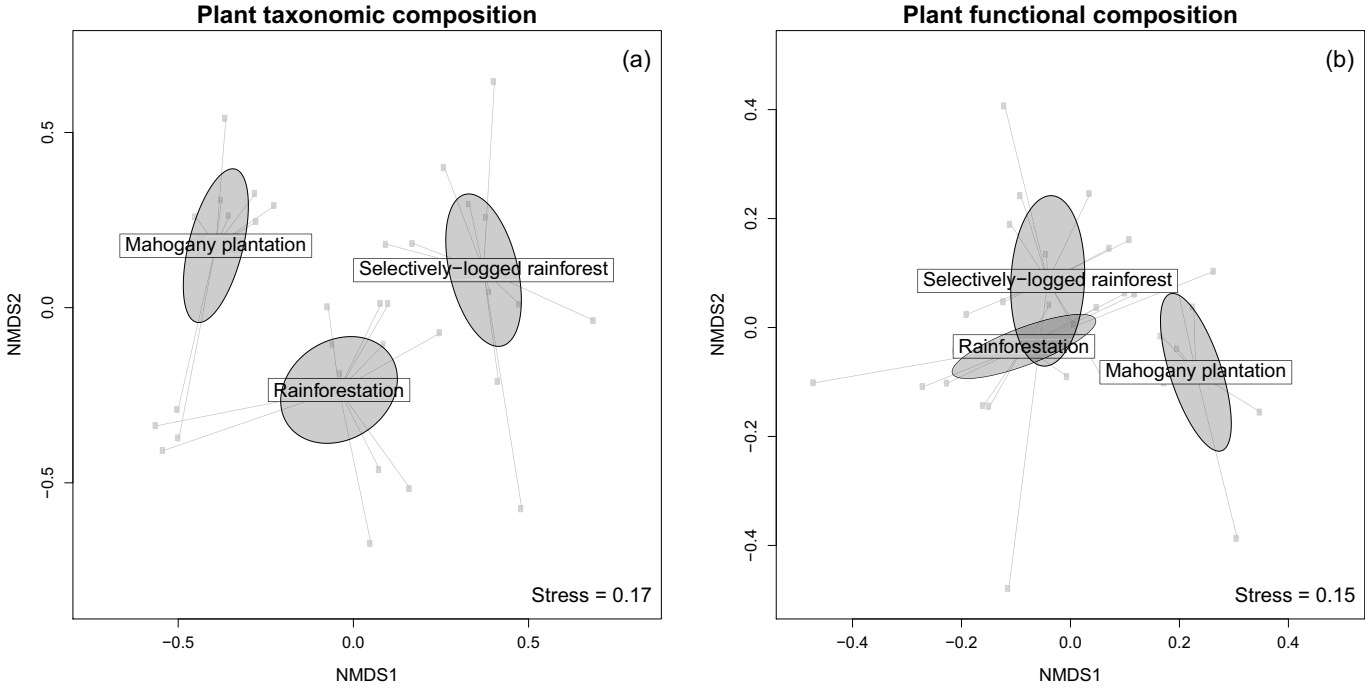

Fig. 5. Two-dimensional non-metric multidimensional scaling using Hellinger distance of forest type differences in understory plant (a) taxonomic composition and (b) functional composition. Mahogany plantations were established as monocultures of *Swietenia macrophylla*, rainforestation plantations were established as high-diversity mixed-species plantings, and selectively-logged rainforests are regenerating native forest with no history of clear-felling. Ellipses represent 95% confidence intervals.

Table 3
Pairwise correlations between aboveground (understory) and belowground functional and taxonomic composition across three land uses on Leyte Island in the Philippines. Values are output from Procrustes superimposition permutation tests, where *r* is a correlation coefficient.

	Plant functional composition	Plant taxonomic composition
Soil microbial composition	$P = 0.001$, $r = 0.52$	$P < 0.001$, $r = 0.53$
Soil microbial function	$P = 0.001$, $r = 0.47$	$P < 0.001$, $r = 0.44$

cannot determine which gram-positive and gram-negative bacterial taxa are dominating in these soils, and so cannot offer a conclusive interpretation of this result. Contrarily, metagenomic analyses provide taxonomic resolution but not reliable biomass estimation, making relative importance estimates of microbial groups more difficult. Combining PLFA and genomic methods, where resources permit, may advance understanding of soil microbial C cycling.

4.1. Soil fungi and SOC

Soil fungal biomass was a strong correlate of SOC concentrations and mirrored SOC across land uses. It is important to point out that causality cannot be established with this correlative data, and indeed SOC concentration could effectuate changes in microbes rather than *vice versa*, or a third, unmeasured factor may be driving their covariance. Experimentally establishing a causal link between microbial composition (or other intermediary soil biological, chemical or physical properties) and SOC concentration in a field setting requires observation of temporal lag (*i.e.* where a change in land use is seen to result in a change in fungal biomass after some time, and in turn a change in fungal biomass is seen to result in a change in SOC). As such, studies are needed in which soil sampling begins at the time of plantation establishment and continues regularly until significant SOC change has occurred. In our experience presented here, this may require studies spanning decades.

The selectively logged rainforests in this study, dominated by trees in the Dipterocarpaceae family, are likely to have significant ectomycorrhizal (ECM) presence (Brearley, 2012), which may in part account for the greater fungal biomass in these forests. Many ECM fungi form belowground fruiting bodies that rely on animals, often small mammals, for spore dispersal (Claridge and May, 1994; Nuske et al., 2018; Schickmann et al., 2012). Even if populations of these animals remain, their movement is restricted in landscapes where forests are separated by agricultural and urban land uses (Eycott et al., 2012; Goosem, 2002). Many ECM fungi with aboveground fruiting bodies are wind dispersed, but in closed forests with limited air flow spores may not move far from their point of origin (Galante et al., 2011). Spore movement over longer distances is more stochastic and may be unreliable for adequate inoculation levels (Peay et al., 2012). Dominated by monocots such as grasses and coconut palms, which are *endo*-(arbuscular)-mycorrhizal (Brundrett, 2009; Rajeshkumar et al., 2015), the baseline land use prior to plantation establishment in our study would have little capacity to support ECM fungi. As such, we speculate that dispersal of ECM fungi into plantation sites is necessary but restricted, so that the capacity for soil microbial restoration by tree planting is limited if unaccompanied by ECM inoculation of plantation seedlings (Aggangan et al., 2012). As the rainforestation plantations were established with several species of Dipterocarp trees, such that 11 out of 77 canopy species were Dipterocarps in 2006 (Nguyen et al., 2012), and had since recruited more in the understory (Wills et al., 2017), a lack of ECM inocula may be a major constraint to the capacity to restore soil microbial function and composition.

The observed covariance between SOC and fungal biomass establishes only correlation, but the mechanistic basis for soil fungi benefiting SOC formation is sound, and informed one of our research hypotheses. Indeed, fungi have good growth efficiency (the conversion of substrate into biomass) (Bonner et al., 2018; Malik et al., 2016), produce stable residues and promote aggregation (Bossuyt et al., 2001; Caesar-tonthat, 2002; Knicker, 2011; Li et al., 2015; Paim and Linhares,

1990; Rillig et al., 2007; Six et al., 2006; Strickland and Rousk, 2010). Malik et al. (2016) found that soils with higher ratios of fungi to bacteria retained more C from litter, seemingly in the form of microbial necromass. Furthermore, fungi may benefit bacterial efficiency by providing structure for bacterial biofilms and chemical power to kick-start decomposition pathways of recalcitrant substrates (De Boer et al., 2005), liable to support whole-community efficiency of soil microbes, and providing more material for SOC formation (Cotrufo et al., 2013). The potential facilitation of bacterial efficiency by fungi may help explain our SOC correlation with fungal biomass rather than fungal to bacterial biomass ratio as originally hypothesised. Even at 40–50 cm depth, SOC correlated positively with fungal biomass measured in the topsoil. Perhaps active fungal mycelia were extending to this depth, which is feasible for many cord-forming basidiomycetes (Stenlid, 2008). Alternatively, enhanced drainage due to greater subsoil organic C (Gageler et al., 2014) (which can only be speculated as we did not measure drainage) could have led to conditions in topsoil that are favourable to fungi.

Soil microbial composition explained more variation in SOC than land use, and once the direct pathway of influence of land use on SOC had been accounted for with a structural equations model, indirect pathways involving changes in microbial composition appeared potentially more influential. We caution against inferring causality from these results, as they are derived from examining covariance structure of a dataset produced by an experimental design not suited for testing causal relationships between soil microbes and SOC. Our findings do, however, robustly indicate that our land use effects on SOC occur overwhelmingly in synchrony with changes in soil microbial composition. That is, the land use effects on soil microbial composition and SOC are so tightly linked in this dataset that the prospect of using one as an indicator of the other seems credible (Shao et al., 2019a, 2019b). Coupled with previous work providing support for microbial composition affecting SOC formation (Bonner et al., 2018; Cotrufo et al., 2013; Kallenbach et al., 2016; Li et al., 2015; Malik et al., 2016; Manzoni et al., 2012; Miltner et al., 2012), and SOC concentration affecting microbial composition (Fierer et al., 2009; Shao et al., 2019b), there are grounds to speculate that restoration of the soil microbial community may be a prerequisite for full recovery of SOC (Shao et al., 2019a).

The relationship between above- and belowground biodiversity is well examined (Hooper et al., 2000; Prober et al., 2015), mostly in temperate ecosystems, but our correlations between above- and belowground function and composition are, to our knowledge, relatively novel for a tropical field setting (but see Bachelot et al., 2016). The extent to which plant traits drive soil microbial recovery *versus* soil microbes drive plant recovery is unclear. Both are likely to influence the other, and feedback loops are liable to make forest restoration more challenging, where restoration of soil depends partially on restoration of plants, but this in turn depends partially on restoration of soil. Two field studies on former arable land in the Netherlands have seen significant benefits to plant community assembly in response to soil inoculations (van der Bij et al., 2018; Wubs et al., 2016). A management solution could be active restoration above- and belowground simultaneously, involving tree planting coupled with soil inoculation. The potential of soil inoculations or transplants to reshape or recover soil microbial communities in a field setting is unknown (Sun et al., 2014), and outcomes across studies so far (which have focused on boreal, temperate, and Mediterranean soils) are not consistent (Calderón et al., 2016; Requena et al., 2001; Wubs et al., 2016; Yergeau et al., 2015). Further research of interventions targeted at microbial recovery may establish if soil microbes should be an integral part of effective restoration of forest ecosystems and their services.

4.2. Limitations of our study

There was considerable site level structural and floristic variation across putative replicates of land uses. This is to be expected in complex human modified environments and in developing tropical countries in particular. An important corollary, however, is that signals in measured variables observable through such background noise are likely to be particularly useful for advancing restoration practice in tropical environments. In this study it appeared that soil fungal biomass provided a strong emergent signal correlating with SOC, which deserves further field testing. If a causal link is established and the relationship better understood, assessment of fungal biomass early after plantation establishment may facilitate forecasting SOC restoration outcomes.

As we examined only one type of mixed-species plantation and one type of monoculture plantation, species effects cannot be disentangled from diversity effects. In the study region, Nguyen et al. (2012) found that monoculture plantations with exotic species, including some of the mahogany plantations sampled here, had significantly higher aboveground productivity than rainforestation plantings. Higher productivity of vegetation generates more C substrate that is available for the formation of SOC. However, if SOC accumulates because input of plant residues outpaces decomposition, then the accumulated SOC ought to resemble undecomposed plant residues. This is generally not the case (Kallenbach et al., 2016; Knicker, 2011; Paim and Linhares, 1990), nor was it so in our study: the C/N ratio of SOC under all land uses was < 16:1, far lower than plant residues (from ~40:1 to > 100:1). Alternatively, higher litter inputs could lead to higher microbial biomass which in turn leads to higher SOC accumulation from microbial residues, but in this study microbial biomass did not differ significantly between land uses at the time of sampling. Soil organic C also did not correlate significantly with standing litter stock after accounting for land use. It appears that microbial decomposition of plant residues in mahogany plantations largely matched input rates and microbial biomass was not measurably stimulated. We thus speculate that the seemingly higher C recovery with mahogany monocultures was not purely a productivity effect.

4.3. Conclusion

We conclude that restoration of tropical forest cover through plantations does not guarantee rapid restoration of the soil microbial community and SOC. A stronger focus on plant community restoration or additional interventions aimed at recovering the soil microbial community, such as soil inoculations, may be needed if more rapid soil restoration is a primary goal. Our study draws attention to the additional challenge to forest ecosystem restoration of soil microbial recovery and the long timeframes required, and further discourages clearing of old-growth forest due to this potential impediment to whole-ecosystem restoration.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2019.06.017.

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