

Changes from pasture to a native tree plantation affect soil organic matter in a tropical soil, Panamá

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Abstract

Background and aims We examined changes in soil organic matter arising from conversion of a 45-year old pasture to a 10 yr. old native tree plantation in Panamá, to evaluate the effect of monoculture and mixtures.

Methods We intensively sampled the soil 0–10 cm depth in the pasture in 2001 and in 22 plantation plots in 2011, ranging from 5 monocultures to 3- and 6-species treatments; samples were also taken from an undisturbed forest site. Soil analyses included organic carbon (SOC) and $\delta^{13}\text{C}$.

Results Conversion of the pasture to tree plantation resulted in an overall loss of SOC of 0.6 kg m^{-2} (18%) in the top 10 cm, but neither tree species nor diversity had a significant effect. End-member $\delta^{13}\text{C}$ values suggested that the contribution of C_3 plants to SOC was increased from 26% in the pasture to 55% after 10 years of plantation and SOC turnover times were calculated to be 21–36 yr.

Conclusions The magnitude of the loss in soil SOC is smaller than the increases in tree biomass ($\sim 3 \text{ kg C m}^{-2}$)

and litter ($\sim 0.3 \text{ kg C m}^{-2}$) in the plantation, but still a significant part of the ecosystem C balance.

Keywords Soil carbon · Soil nitrogen · $\delta^{13}\text{C}$ · Soil C turnover time · Tropical forest · Afforestation

Introduction

Changes in land-use and land-cover can have significant effects on soil organic carbon (SOC) and Sanderman et al. (2017) have recently suggested that conversion of native vegetation to agriculture globally has generated a loss of over 100 Pg of SOC. There are, however, large variations in the magnitude of change in SOC. Powers et al. (2011) collated data from 80 studies examining the effect of land-use change in the tropics on SOC and showed that there were significant increases or decreases in 8 of the 14 change categories. The change from forest to pasture resulted in an average increase in SOC mass in the top 10 cm of $\sim 13.7\%$ (standard deviation 28.2, $n = 118$) and the increase averaged $\sim 4.8\%$ (s.d. 24.1, $n = 27$) when pasture was converted to plantation. Powers et al. (2011) suggested that mean annual precipitation and clay mineralogy were important controls on the magnitude of the change. Marín-Spiotta and Sharma (2013) have also demonstrated the very varied response of SOC to land-use change to plantation and successional forests in the tropics, and identified a similar range of variables influencing the SOC. In another meta-analysis, Don et al. (2011) emphasized the importance of changes in bulk density with land use and

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reported average changes in SOC mass in the top 10 cm of a loss of ~12% from primary forest to grassland and a gain of ~12% from grassland to secondary forest.

Conversion of tropical pastures to plantations has occurred, either for commercial wood production, such as teak, or for native tree species to enhance biodiversity. This change in land-use promotes C sequestration in the vegetation, but may decrease or increase the SOC. Silver et al. (2004) reported that reforestation of pastures in Puerto Rico resulted in an average gain of SOC of 1.3 kg m^{-2} in the top 10 cm and 3.4 kg m^{-2} in the top 60 cm over 61 years, but that tree species and diversity had no discernable effects on the SOC. Most of the increases in SOC occurred after 22 years.

The changes in SOC result from differences in the input and decomposition of plant litter and roots. Where land-use change involves pastures and trees, identification of changes in the SOC $\delta^{13}\text{C}$ value (based on the $^{13}\text{C}/^{12}\text{C}$ ratio) can be used to calculate the gain and loss of the grass and tree derived SOC. The strong separation of $\delta^{13}\text{C}$ value in forests (dominantly C_3 plants, ~–28‰, SOC_3) and pastures (dominantly C_4 plants, ~–13‰, SOC_4), has been successfully used to calculate gains and losses. In the Puerto Rico study, for example, Silver et al. (2004) found that in the top 10 cm, the pasture SOC was derived dominantly (83%) from C_3 plants, while after 61 years for tree growth, this was reduced to 29%. Changes in the proportion of C_3 and C_4 -derived SOC can be used to estimate decomposition rates and thus turnover times (e.g. Balesdent and Mariotti 1996).

Evaluation of the changes in soil properties brought about land-use can be made either through following the change at one location through time or by substituting space for time in a chronosequence which assumes soil properties were similar before the land-use change (e.g. Davidson and Ackerman 1993; Veldkamp 1994). In both approaches, the large spatial variability in soil properties restricts the attribution of a difference in soil properties to the land-use change (Allen et al. 2016). Thus, some knowledge of the characteristics of the spatial variability of soil properties is needed to adequately define a sampling strategy.

In Sardinilla, central Panamá, a 45 year-old pasture was converted to a native tree plantation in 2001 with a biodiversity experimental design (Scherer-Lorenzen et al. 2005). Its aim was to compare the productivity of mixed-species plantations with monocultures to test whether diversity would enhance productivity and hence C storage (Potvin et al. 2011). This provided an

opportunity to examine changes in soil properties, particularly the SOC and soil nitrogen (SN) content and mass, and $\delta^{13}\text{C}$ value associated with land-use changes from pasture to plantation and the effect of plantation species and mixture. In nearby Barro Colorado Island (BCI), an undisturbed forest provided an opportunity to estimate the surface soil properties of a site that may have been similar to the precursor of the Sardinilla pasture.

To meet these objectives, we intensively sampled the 0–10 cm layer of the Sardinilla pasture soil in 2001 to establish spatial variability and sampled 7 soil profiles to a depth of 100 cm. We repeated the 0–10 cm sampling in the plantation in 2011 within the experimental diversity design of 7 treatments, at locations close to those sampled in 2001. We also sampled the 0–10 cm layer in the tropical forest soil. Analysis of vegetation from the pasture, the plantation and the tropical forest provided $\delta^{13}\text{C}$ values which combined with the $\delta^{13}\text{C}$ values of the soil allowed an estimate of the contribution of C_3 and C_4 plants in trees and pasture, respectively, to the SOC and the calculation of SOC turnover time.

Materials and methods

Study sites

Central Panamá receives about 250 cm of precipitation annually, of which 220 cm falls in the rainy season from May to November; the mean annual temperature is 25° C. At the Sardinilla site (9°19' N, 79°38' W), at an elevation of ~70 m above sea level (a.s.l.), the original forest vegetation site was cleared in 1952/1953. It supported 2 years of crops (e.g. corn, rice, plantain and yucca) before being converted to pasture and was grazed for ~45 yr. The major species are *Cynodon dactylon*, *Scleria malaleuca* and *Ishalum indicum* with patches of the invasive grass *Saccharum spontaneum*.

In 2001, a plantation using native tree species was established on 7.5 ha of the pasture with an average of 1141 stems ha^{-1} . The six native tree species used were *Luehea seemanii* (Ls), *Anacardium excelsum* (Ae), *Hura crepitans* (Hc), *Cedrela odorata* (Co), *Tabebuia rosea* (Tr) and *Cordia alliodora* (Ca). There was high mortality in *C. alliodora*. Twenty-four diversity plots of 0.21 ha were planted: six 6-species (A), six 3-species (T) and twelve monocultures (Scherer-Lorenzen et al. 2005). The levels of diversity were randomly assigned

to all plots in the landscape, except for the Tr and Ae monocultures that were placed in the wetter east flank of the plantation due to their ability to tolerate waterlogged soils (see Fig. 1 in Healy et al. 2008). To avoid excessive water logging in the lower lying plots, drainage ditches were dug in 2002. A moderately dense understory vegetation (shrubs, grasses and sedges) is present in the plantation, which is cut once a year (typically in December) and the residues left on-site. The soils at Sardinilla are derived from Tertiary limestone and other sedimentary rocks and are generally clayey Cambisols or Tropudalfs (Soil Survey Staff 1990) with moisture status varying greatly from the dry to wet seasons.

On Barro Colorado Island (BCI) located 40 km southwest of Sardinilla, the site (9°09' N, 79°51' W) was located in a semi-deciduous old-growth forest, underlain by limestone bedrock (Leigh et al. 1996) at an elevation of ~ 130 m a.s.l. and with a slope of 5%. Vegetation in the region was a result of shifting agriculture practiced until the decimation of native populations during the Spanish Conquest when agriculture in the region was abandoned and returned to forest (Leigh et al. 1996) and may be similar to the vegetation of the Sardinilla site prior to clearance. The soils are Cambisols (Grimm et al. 2008; WRB 2006).

Soil sampling

The soils in the Sardinilla pasture were sampled in June 2001, about one month after the start of the rainy season and just prior to tree planting. The top 10 cm was collected using a metal cylinder 5 cm in diameter, pushed into the soil surface, after removal of the litter. Because of the heavy texture of the soil, some

compaction (1 to 2 cm) of the soil occurred in the cylinder, but this was mainly in the upper 5 cm and inspection showed that the full 10 cm was sampled. Surface soils were sampled along a 15 m grid, offset 1.5 m from the grid in which the trees were to be planted, to allow resampling after the trees had been planted. A telescopic grid network was located in one mid-slope 15 × 15 m block, in which a 3 × 3 m grid was sampled at 1 m intervals, followed by a 1 × 1 m grid sampled at 0.25 m intervals. Overall, 380 surface soil samples were collected. In addition, seven soil profiles dug down to 100 cm were sampled, located to represent the major topographic zones, of top-, mid- and bottom-slope positions. Composite samples of four 5 cm-deep core samples were taken from pit walls at the 5 and 10 cm depths and two were taken at 10 cm intervals between from 20 to 100 cm. Litter was collected from thirty 25 × 25 cm quadrats across the topographic gradient in the pasture and samples of the main grass species were also obtained.

In June, 2011, surface soils in the plantation were resampled within the native tree plantation experimental treatments by relocating (estimated error ± 5 m) the points sampled in 2001. Four samples were collected on the 15 × 15 m grid for each of the 22 treatment blocks (Ca plots were not sampled owing to *C. alliodora* mortality), resulting in 88 surface soil samples. At each of these 88 points, a 25 × 25 cm quadrat was used to collect understory biomass and litter on the soil surface; the soil sample was collected from the centre of this quadrat. Samples of senescent leaves and roots of the five plantation tree species were collected for analysis of C and N content and $\delta^{13}\text{C}$ value.

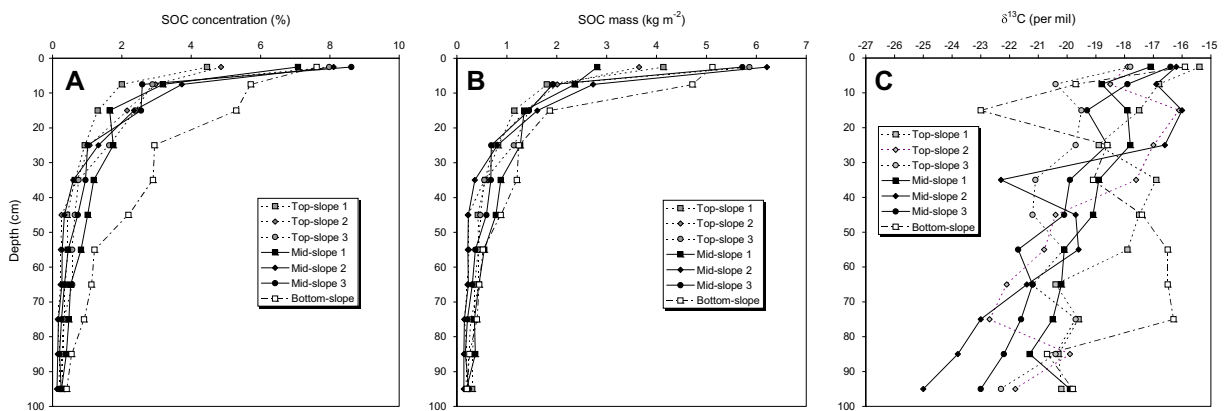


Fig. 1 Distribution of soil properties with depth in the seven profiles sampled at the Sardinilla pasture in 2001: **a** SOC concentration; **b** SOC mass per 10 cm depth increment; **c** $\delta^{13}\text{C}$ value

At the BCI site, a 12×12 m plot was established in 2002, with surface soil samples collected at 3 m intervals and a nested sampling at 1 m spacing within one 3×3 m plot and sampling at 0.2 m spacing within one 1×1 m block. This resulted in 70 soil samples and litter was collected from two 1×1 m quadrats and composited.

Soil and vegetation analyses

The soil samples had fine roots removed and weighed after oven-drying at 60°C and then the soil was weighed fresh, air-dried to calculate gravimetric and volumetric field moisture content and bulk density. Samples were homogenized by hand, ground to break up aggregates and analyzed for pH in H_2O with a 1:2 soil:water ratio (Carter 1993). Concentration of SOC and SN and $\delta^{13}\text{C}$ value were analyzed using continuous-flow isotope ratio mass spectrometry on a Carlo Erba Elemental Analyzer connected to an Isoprime Mass Spectrometer. pH measurements showed that carbonates were not present in the surface soil samples (Abraham 2004). Concentrations of SOC and SN were combined with bulk density to estimate SOC and SN mass (kg m^{-2}) of the top 10 cm. Particle size distribution was measured on selected samples by the pipette method (Carter 1993). Samples of vegetation and litter were oven-dried at 60°C , ground in a Wiley Mill and analyzed for C and N concentration and $\delta^{13}\text{C}$ value, as above.

The fraction of C_3 -plant and C_4 -plant derived SOC (SOC_3 and SOC_4 , respectively) was calculated using a two-compartment mixing model (Balesdent and Mariotti 1996). Changes in the SOC_4 fraction in the BCI forest to Sardinilla pasture and in the SOC_3 fraction in the Sardinilla pasture to plantation were used to estimate the decomposition rate (k) using logn transformation of initial and final values and 45 and 10 yr, respectively, and these rates were then used to estimate the turnover time ($1/k$).

Statistical analyses

Spatial variability of the 0–10 cm surface soil samples collected from the two grids in the pasture was assessed by calculation of mean and standard deviation. The larger scale variation in soil properties for the pasture in 2001 and the native tree plantation in 2011 were determined from the 88 locations sampled in 2011, by calculating semi-variogram parameters using Matlab v2013b and ArcGIS 10.1.

To determine the effects of forest conversion to pasture on soil parameters we compared BCI with 2001 Sardinilla soils before the tree plantation was established using the non-parametric Mann-Whitney U-test, as the BCI data were not normally distributed. The same test was also used to compare plantation soils 10 years after tree planting with BCI soils to determine how closely soils from a reforested system compare to undisturbed forest. The impact of conversion from pasture to forest on soil parameters was evaluated either 1) using a paired t-test or the non-parametric equivalent Wilcoxon signed ranks test, comparing Sardinilla soils prior to tree planting with those 10 years after tree planting; or 2) using analysis of variance (ANOVA) with time and its interaction with diversity and species effects as factors (see below).

ANOVAs with diversity, sampling year and their interaction were used as factors to test for differences in soil parameters among diversity plots (monoculture, three-species, and six-species plots) across sampling years (2001 and 2011). To test for species-specific effects on soil parameters (tree species identity), samples from only the monoculture plots of each the five species were compared, with tree species (Ae, Co, Hc, Ls and Tr), sampling year (2001 and 2011) and their interaction used as factors in the analysis. One-way ANOVA was used to test for diversity and tree species identity effects on vegetation parameters (litter, understory biomass, and root biomass) collected in 2011. Bonferroni pairwise comparisons were used as post hoc tests when necessary. Linear regression analysis was used to test the relationships between soil and vegetation parameters. All statistical analyses were performed using SYSTAT v. 10.0.

Results

Spatial variability of soil properties

Sampling within the two grids at the Sardinilla pasture in 2001 showed that within a 1×1 m grid at 25 cm interval, the coefficient of variation of soil properties ranged from 0.01 to 0.15, being smallest for pH and C:N ratio and largest, unfortunately as they are the properties of primary interest, for C and N% and SOC and SN mass (Tables 1 and 2). A similar variation was observed when a larger grid (3×3 m) was sampled. Thus, the effect of changes in land use on soil properties will have

Table 1 Small-scale variability in properties in the 0 to 10 cm soil samples collected from 1 × 1 m (*n* = 25) and 3 × 3 m (*n* = 58) grids in the Sardinilla pasture, 2001

Grid	Bulk density (g cm ⁻³)	pH	SOC (%)	SOC mass (kg m ⁻²)	N (%)	SN mass (kg m ⁻²)	C:N ratio	δ ¹³ C (‰)
1 × 1 m								
Mean	0.482	5.42	7.40	3.54	0.65	0.313	13.4	-17.0
SD	0.047	0.07	1.08	0.42	0.09	0.039	0.2	0.8
CV	0.098	0.013	0.146	0.119	0.138	0.125	0.015	-0.047
3 × 3 m								
Mean	0.489	5.61	7.04	3.42	0.61	0.297	13.45	-16.7
SD	0.049	0.26	1.17	0.49	0.10	0.044	0.4	1.0
CV	0.100	0.046	0.166	0.143	0.164	0.148	0.030	-0.060

to be larger than this small-scale variability to be detectable.

From the semi-variogram analysis of the 88 soil samples collected in 2001 and 2011, the range (distance beyond which there is no spatial autocorrelation) is approximately 30 m, apart from N% measured in 2011, which has a range of 51 m (Table 2). The nugget values are small for all measured properties, indicating small microscale variation and/or measurement error, except for N% in 2001 where the relative nugget effect (ratio of the nugget to the sill) is 8%. The values of the sill indicate the overall variation after adjusting for possible correlations in the closely-spaced sample points (inherent variation in samples where there is no more autocorrelation). The standard deviation column (square root of the sill) is more easily interpreted because the units are the same as the measured parameter.

Soil profiles in the Sardinilla pasture

In the Sardinilla pasture, the seven soil profiles sampled in 2001 showed a decrease in SOC concentration with depth, from an average of 7.0% at 0 to 5 cm to 0.3% at 90 to 100 cm; there was a steep decline within the top 20 cm (Fig. 1a). Dry bulk density ranged from 0.7 to 1.0 g cm⁻³ in the top- and mid-slope profiles and 0.4 to 0.6 g cm⁻³ in the bottom slope profile. The soil profiles down to 100 cm contained between 10 and 17 kg C m⁻², increasing downslope, and the surface 10 cm contained an average of 43% of the SOC to a depth of 1 m (Fig. 1b). As rooting depth in these heavy textured soils is shallow (most roots occurred in the top 20 cm), this is likely to be the section of the soils showing the greatest change to land-use. The δ¹³C value in the pasture profiles generally decreased with depth, from an average of

Table 2 Semi-variogram characteristics of properties at the 88 locations sampled across the 2001 pasture and the 2011 plantation. Standard deviation = SD, Coefficient of variation = CV

Property	Range (m)	Sill (variance)	Nugget	SD
2001				
SOC (%)	33.0	1.506	1.865E ⁻¹⁰	1.227
SOC mass (kg m ⁻²)	31.2	0.351	3.097E ⁻¹²	0.593
SN (%)	28.9	0.009	1.48E ⁻¹³	0.095
SN mass (kg m ⁻²)	32.5	0.003	3.55E ⁻¹³	0.055
δ ¹³ C (‰)	30.6	0.992	3.82E ⁻¹²	0.996
2011				
SOC (%)	35.9	0.726	6.871E ⁻¹¹	0.852
SOC mass (kg m ⁻²)	30.3	0.148	8.780E ⁻¹¹	0.384
SN (%)	51.0	0.006	0.0004	0.076
SN mass (kg m ⁻²)	33.7	0.001	1.428E ⁻¹²	0.032
δ ¹³ C (‰)	39.2	1.171	2.896E ⁻¹¹	1.082

–17.5‰ in the top 10 cm to –21.7‰ at 90 to 100 cm (Fig. 1c).

The surface soils in the Sardinilla pasture had a clay loam texture, containing an average of 4, 30, 44 and 21% sand (0.02–2 mm), silt (0.002–0.02 mm), clay (0.002–0.0002 mm) and fine clay (< 0.0002 mm), respectively. At the BCI site, the soil was a sandy loam, with 32, 33, 24 and 11% of the above fractions, similar to the Marron unit reported by Grimm et al. (2008).

Effect of land-use change on soil properties

Following 10 yr of tree growth at the Sardinilla plantation, overall (88 samples) there were significant decreases in bulk density by 5% ($t = -5.04$, $p < 0.001$), percent SOC by 13% ($t = -4.94$, $p < 0.001$), percent SN by 6% ($t = -2.68$, $p = 0.009$) and C:N ratio by 21% (Wilcoxon signed rank test, $p < 0.001$) (Table 3). There were smaller masses of SOC and SN in the plantation soil, by 18 and 11%, respectively. The $\delta^{13}\text{C}$ signature had decreased by 4.3‰ ($t = -4.94$, $p < 0.001$) from the pasture values. The BCI forest soil had a significantly lower bulk density, percent and mass of SOC and SN, C:N ratio and $\delta^{13}\text{C}$ value than the Sardinilla pasture.

The C:N ratio of above-ground vegetation inputs averaged 30:1, while the roots of the plantation trees averaged 62:1 (Table 4).

Overall, neither tree species diversity nor tree species identity had a significant impact on soil properties after 10 yr (Table 5). While there were significant differences among diversity plots for C:N ratio ($p = 0.034$), these differences were present in 2001 before tree planting and were maintained in 2011 (i.e. no significant

Table 4 C and N content and $\delta^{13}\text{C}$ value of BCI litter, Sardinilla pasture litter and Sardinilla plantation trees and understorey

Plant tissue	C (%)	N (%)	C:N ratio	$\delta^{13}\text{C}$ (‰)
BCI litter	44.0	1.47	29.9	–29.4
Sardinilla pasture 2001				
Pasture litter (range and mean)	41.5	1.30	31.9	–11.6 to –16.0, –13.5
Plantation trees 2011				
Ae leaves	44.5	1.01	44.1	–29.7
Ae roots	44.1	0.51	86.5	–27.5
Co leaves	48.0	1.58	30.4	–32.0
Co roots	45.6	1.38	33.0	–30.2
Hc leaves	45.0	1.68	26.8	–28.8
Hc roots	43.9	1.10	39.9	–28.2
Ls leaves	47.7	1.01	47.2	–29.5
Ls roots	46.5	0.76	61.2	–28.8
Tr leaves	48.0	1.53	31.4	–29.4
Tr roots	47.9	0.53	90.4	–28.4
Plantation understorey 2011				
Plants (range)	45.55	1.60	28.4	–11.1 to –33.1

interaction between diversity effect and time). Similarly, monoculture plots of the five species significantly differed in percent SOC ($p = 0.001$), dry bulk density ($p < 0.001$), pH ($p < 0.001$), and C:N ratio ($p < 0.001$), but these were the result of differences present before tree planting which were still present in 2011. The only exception was soil moisture, which was significantly different among monoculture plots ($p < 0.001$) and showed a significant interaction through time ($p < 0.001$). In this case, Ls monocultures plots

Table 3 Comparison of soil properties, 0 to 10 cm, at BCI forest 2002, Sardinilla pasture 2001 and Sardinilla plantation 2011, as mean with standard deviation in parentheses

Site and sampling date	<i>n</i>	Bulk density (g cm ⁻³)	pH*	SOC (%)	SOC mass (kg m ⁻²)	SN (%)	SN mass (kg m ⁻²)	C:N ratio	$\delta^{13}\text{C}$ (‰)#	SOC ₃ (%)^
BCI forest 2002	61	0.50 (0.09)	6.11 (0.40)	4.52 (1.63)	2.19 (0.54)	0.44 (0.11)	0.23 (0.04)	12.0 (1.2)	–26.93 (0.58)	93
Sardinilla pasture 2001	380	0.57 (0.12)	4.82 (0.38)	5.89 (1.51)	3.33 (0.67)	0.49 (0.13)	0.28 (0.06)	14.1 (1.5)	–16.94 (0.99)	27
Sardinilla plantation 2011	88	0.54 (0.06)	4.80 (0.41)	5.12 (0.84)	2.72 (0.39)	0.46 (0.08)	0.25 (0.04)	11.1 (0.9)	–21.21 (1.05)	55

*BCI forest 2002 and Sardinilla pasture 2001 pH measured using 1:10 soil:water ratio, Sardinilla pasture 2001 88 points sampled in 2011 and Sardinilla plantation 2011, 1:2 soil:water ratio

$\delta^{13}\text{C}$ Sardinilla 2001 for all 88 2011 locations

^ SOC derived from C₃ plants assuming $\delta^{13}\text{C}$ end members of –28‰ (C₃) and –13‰ (C₄), respectively

Table 5. Understory and litter mass, tree litter decomposition rate (k derived from Scherer-Lorenzen et al. 2007) and soil characteristics (0 to 10 cm) of the 2011 Sardinilla plantation plots as overall mean (4 samples collected from within each plot, number of plots sampled indicated) with standard deviation in parentheses. Treatments are for mono-specific plots (Ae, Co, Hc, Ls and Tr) and 3-species (A) and 6-species (T) plots

Treatment (# plots sampled)	Understory biomass (kg m ⁻²)	Litter (kg m ⁻²)	Root biomass (g m ⁻²)	k (yr ⁻¹)	SOC (%)	SN (%)	SOC mass (kg m ⁻²)	SN mass (kg m ⁻²)	$\delta^{13}\text{C}$ (‰)	SOC ₃ (%)
Ae (2)	0.32 (0.17)	0.59 (0.17)	53.9 (44.4)	1.31	5.72 (0.90)	0.47 (0.09)	2.94 (0.51)	0.24 (0.05)	-21.16 (0.67)	54.4 (4.5)
Co (2)	0.78 (0.38)	0.39 (0.13)	31.3 (25.0)	2.23	4.50 (0.64)	0.42 (0.07)	2.61 (0.32)	0.24 (0.04)	-21.26 (0.94)	55.1 (6.4)
Hc (2)	0.60 (0.26)	0.25 (0.17)	46.8 (43.4)	7.34	5.34 (0.62)	0.45 (0.06)	2.71 (0.22)	0.23 (0.03)	-21.55 (1.52)	57.0 (10.2)
Ls (2)	0.32 (0.24)	0.45 (0.16)	12.1 (12.8)	1.79	5.04 (0.62)	0.43 (0.05)	2.71 (0.28)	0.23 (0.03)	-20.34 (1.21)	48.5 (8.0)
Tr (2)	0.35 (0.14)	0.35 (0.11)	27.3 (24.2)	2.70	4.96 (0.96)	0.49 (0.10)	2.77 (0.41)	0.27 (0.05)	-20.74 (0.64)	51.6 (4.2)
A (6)	0.22 (0.14)	0.50 (0.20)	25.1 (41.0)	-	5.24 (0.59)	0.48 (0.05)	2.81 (0.32)	0.26 (0.03)	-21.45 (0.95)	56.3 (6.3)
T (6)	0.43 (0.27)	0.50 (0.23)	21.2 (30.1)	-	5.01 (1.07)	0.46 (0.09)	2.60 (0.47)	0.24 (0.04)	-21.29 (1.07)	55.3 (7.1)

became drier and Tr monocultures became wetter relative to the other species monocultures from 2001 to 2011.

Unlike soil properties, tree diversity and tree species effects were significant for understory and fine root biomass in 2011 (Table 5). Understory and root biomass were significantly different among diversity plots, with greater understory biomass in 3-species than 6-species plots ($T > A$, $F = 3.50$, $p = 0.035$) and greater root biomass in monocultures than 3-species plots ($F = 3.82$, $p = 0.026$). There were also significant differences in root biomass and understory biomass among monoculture plots, with Ls plots having significantly less root biomass than Ae or Hc plots ($F = 4.065$, $p = 0.008$) and Tr plots having significantly greater understory biomass than Ae, Hc or Ls ($F = 8.64$, $p < 0.001$).

The litter obtained in the tree plantation in 2001 ranged from 0.25 to 0.59 kg m⁻², equivalent to 0.12 to 0.30 kg C m⁻², and much larger than the litter in the heavily grazed pasture sampled in 2001. In the tree plantation there was a negative exponential relationship between litter mass and decomposition rate of tree leaves ($y = 0.558e^{-0.116k}$, $r^2 = 0.80$, $p = 0.025$, $n = 5$; Table 5). The smallest litter amounts were found in the Hc and Tr monocultures (0.25 and 0.35 kg m⁻²) which had the fastest litter decomposition rates (exponential decay or k value of 7.3 and 2.7 yr⁻¹, respectively, Scherer-Lorenzen et al. 2007), while the largest litter amounts were found in the Ae and Ls monocultures (0.59 and 0.45 kg m⁻²), which had the slowest litter decomposition rates ($k = 1.3$ and 1.8 yr⁻¹, respectively).

Origin of SOC and turnover time

In the 2001 Sardinilla pasture, there was a mixture of C₄ and C₃ plants, whose $\delta^{13}\text{C}$ value ranged from -12.0 to -28.2‰ and the litter collected from a mixture of top-, middle- and bottom-slope sites averaged -13.5‰ (Table 4). In the 2011 plantation, the $\delta^{13}\text{C}$ of the 5 tree species ranged from -28.8 to -32.0‰ in senescent leaves and -27.5 to -30.2‰ in roots. The $\delta^{13}\text{C}$ ranged from -11.1 to -33.8‰ in understory plants, though C₄ plants were dominant. The $\delta^{13}\text{C}$ signature of litter collected from the forest plot at BCI averaged -29.4‰. Thus, there are some uncertainties regarding the $\delta^{13}\text{C}$ value of the end members of organic matter input for the pasture, the plantation and the BCI forest. Here we use estimates of -28.0 and -13.0‰ to calculate the proportion of SOC attributed to C₃ (SOC₃) and C₄ (SOC₄)

Table 6 Changes (Δ) in estimated mass (kg m^{-2} , mean and standard deviation) of C_3 - and C_4 -derived SOC (SOC_3 and SOC_4) in 0–10 cm soil, from conversions of BCI forest to 2001 pasture to 2011 plantation, assuming $\delta^{13}\text{C}$ end-members of -28 and -13‰

BCI mass	Sardinilla 2001 mass	Δ BCI – Sardinilla 2001	Sardinilla mass 2011	Δ Sardinilla 2001–2011
SOC_3				
2.19 (0.53)	0.72 (0.23)	-1.47	1.49 (0.30)	0.77 (0.25)
SOC_4				
0	2.50 (0.54)	2.50	1.23 (0.24)	-1.27 (0.56)

origins, respectively, and the loss or gain of these amounts in the top 10 cm of soils through the two changes in land use.

The conversion of the Sardinilla pasture to the plantation over 10 yr caused a loss of 1.27 kg C m^{-2} of C_4 -derived SOC and a gain of 0.77 kg C m^{-2} of C_3 -derived SOC (Table 6). If the BCI soil is the same as the forest soil at Sardinilla, this would entail a loss of 1.47 kg C m^{-2} of C_3 -derived SOC, and a gain of 2.50 kg C m^{-2} of C_4 -derived SOC, over 45 yr. These changes can be used to estimate the turnover times of the SOC in 0–10 cm. For 10 yr conversion of the pasture SOC_4 to plantation the estimate is 21 yr and the 45-yr conversion of BCI SOC_3 to the pasture provides an estimated turnover time of 36 yr.

Discussion

As anticipated, our study has shown the high degree of spatial variability in soil properties that can occur within short distances even where land use was constant, such as the Sardinilla pasture. Much of the variability occurs at small distances, as shown by the comparison of variability within 1 and 9 m^2 (Table 1) and at a broader scale, the range values are large (Table 2). This is a common phenomenon in soils (e.g. Webster and Oliver 1992) limiting our ability to detect changes associated with variations in land-use across landscapes, in substituting space for time in chronosequences and in conducting longitudinal studies at the same site, as at Sardinilla (e.g. Allen et al. 2016; Powers and Schlesinger 2002). Thus, to be able to detect significant differences in soil properties, a substantial number of replicate soil samples are needed: Allen et al. (2016) suggest 4 to 8 replicates per treatment in a study of land-use change effects in Indonesia. In our study, we took 4 soil samples per $30 \times 30 \text{ m}$ treatment plot and each treatment was replicated between 2 and 6 times. The small nugget values across sampling dates and soil properties suggest

minimal random measurement errors and smooth spatial continuity between neighbouring points (Vieira and Gonzalez 2003). A low nugget/sill ratio indicates strong spatial correlation. In general, between 2001 and 2011 the variance of the characteristics decreased (except $\delta^{13}\text{C}$) and range values increased, suggesting an increase in uniformity of the characteristics through time. Changes over time in range values can be attributed to different processes, parameters or structures affecting the soil characteristics (Korres et al. 2015). In this case, the change in the range parameter for $\text{N}\%$ from 29 to 51 m could reflect an homogenization of the soil, possibly associated with the change from variable grazing in the pasture to a more uniform tree cover.

The Sardinilla pasture soil contained an average of 3.3 kg m^{-2} of SOC within the upper 10 cm of the profile, similar to mean values of 3.2 and 3.8 kg m^{-2} obtained by Powers et al. (2011) and Marín-Spiotta and Sharma (2013) for tropical clay-rich forested and plantation soils. The 10 to 17 kg m^{-2} SOC stored within the 100 cm deep profiles is also similar to the averages of 12 and 16 kg m^{-2} reported by Powers et al. (2011) and Marín-Spiotta and Sharma (2013). The shallow rooting in the heavy textured Sardinilla soil prevents large accumulations of C at depth.

Several meta analyses have shown the large variability in response of soil organic matter to changes in land-use in the tropics (e.g. Guo and Gifford 2002; Don et al. 2011; Powers et al. 2011; Marín-Spiotta and Sharma 2013), resulting from differences in input of plant litter above- and below ground and rates of decomposition in the soil. Variables such as climate, type of land-use change, soil type and duration of change influence the direction and magnitude of changes in SOC. Our estimates of SOC mass change in the change from forest to pasture and pasture to plantation fall within the range of published observations. There are two caveats to our results, however.

First, the difference in clay content between the surface BCI forest and Sardinilla soils (35 and 65%,

respectively) means that the SOC mass in the former is probably an underestimate of what it would be if the clay content had been 65%; thus the change in SOC mass from forest to pasture (gain of 1.14 kg m^{-2}) is likely an overestimate. Second, differences in bulk density of the top 10 cm soil entails the possibility of errors in extracting the same amount of soil under the varying land uses. Our values of a 14% increase in bulk density 0–10 cm in converting from forest to pasture and a decrease of 5% in conversion from pasture to plantation are similar to the averages cited by Don et al. (2011). As noted by Ellert and Bettany (1995), an increase in bulk density when sampled to the same depth could increase the SOC mass. Sampling to a common soil horizon would avoid this problem, but in these tropical soils there is no strong horizon development. The difference in bulk density between the Sardinilla pasture and plantation soils is 0.03 g cm^{-3} (or 5% of the pasture value) and this may contribute to the observed loss of 18% of SOC. Similarly, the difference in SOC mass between BCI and pasture soils (and increase of 52%) may partially arise from the difference in bulk density of 0.07 g cm^{-3} (or 14%).

While the $\delta^{13}\text{C}$ value in the uppermost layers of the pasture soil is associated with the change of input from forest to pasture (Table 5), the variable increase in $\delta^{13}\text{C}$ value with depth (from averages of -17.5‰ at 0–10 cm to -21.7‰ at 90–100 cm) is similar to that reported for pasture soils in BCI (Schwendenmann and Pendall 2006) and Puerto Rico (Marín-Spiotta et al. 2009; Silver et al. 2004). There are several possible causes, including differences in the input of C_3 and C_4 plant roots and the root-derived legacy from the forest, as well as differences in the rate of decomposition of organic matter leaving a residue richer in ^{13}C with a larger $\delta^{13}\text{C}$ value, and DOC percolating down through the profile and being adsorbed on to clay surfaces (see Boström et al. 2007). However, in none of the pasture profiles does the $\delta^{13}\text{C}$ value increase with depth, as commonly observed under forested soils, nor reach a value associated with organic matter derived from the forest.

The estimated turnover time of SOC in the top 10 cm of the soil of 36 and 21 yr for the SOC_4 and SOC_3 fractions under changing land use from forest to pasture and pasture to plantation is similar to values found in tropical soils reported by Giardina and Ryan (2000). Schwendenmann and Pendall (2006) estimated 69 and 123 yr (0–5 and 5–10 cm depths, respectively) for a 90-yr old conversion of forest to pasture in a well-drained

soil on BCI, and also demonstrated that the turnover time varied with aggregates in the soil. In Costa Rica, Huth et al. (2012) reported that conversion of forest to pasture resulted in about half of the SOC in the top 40 cm turning over in 40 to 50 yr. Depending on the $\delta^{13}\text{C}$ value ascribed to litter input, Marín-Spiotta et al. (2009) estimated turnover times of 40 to 80 yr in the 0–10 cm depth of soils undergoing conversion from pasture to forest in Puerto Rico, and also noted that the turnover time varied among density fractions in the mineral soils.

Although considerable attention has been given to the role of biodiversity on litter decomposition (e.g. Handa et al. 2014; Hättenschwiler et al. 2005), our results suggest that the litter in the Sardinilla plantation, after 10 years, reflects primarily the speed of decomposition of the leaves of the 5 tree species, especially the fast rate of *H. crepitans* (Table 5). The biodiversity plots had litter amounts similar to those found under *A. excelsum* and *L. seemanii*, which had the slowest rates of litter decomposition (Scherer-Lorenzen et al. 2007). Silver et al. (2004) also noted that the forest floor C pool did not vary significantly with plant community characteristics in a 55–60 yr conversion of pasture to various tree species in Puerto Rico.

There are distinct differences in SOC concentration and mass, and to a lesser extent SN concentration and mass, in the top 10 cm of the soil in land use conversion from pasture to plantation (Table 3), however, there is little evidence that tree species and biodiversity play a significant role in SOC or SN in the plantation after 10 yr, beyond patterns already established before the plantation. It may take longer for a soil pattern to develop; we observed significant differences in fine root biomass among the plantation treatments and this may be a major source of SOC and SN, in addition to leaf litter decomposition and incorporation into the soil. Guerrero-Ramírez et al. (2016) measured rates of root decomposition (over 1.3 yr) at a depth of 20 cm in Sardinilla with k values ranging from with varying from 0.4 to 1.1 yr^{-1} , considerably slower than the values of 1.3 to 7.3 yr^{-1} for tree litter (Scherer-Lorenzen et al. 2007). However, the root decomposition rates were unaffected by tree species richness, either by species manipulation within litter bags or as a function of varying tree overstory richness.

In 2009, the aboveground biomass in the Sardinilla plantation was estimated to be between 1.8 and 2.3 kg C m^{-2} , with an increase from mono-specific to 3- and 6-

species plots, dominated by the tree cover (Potvin et al. 2011). This contrasts with an estimated aboveground biomass of 10–15 kg C m⁻² in the BCI forest (Chave et al. 2003; Leigh et al. 1996) and 0.2 kg C m⁻² in the pasture (Wolf et al. 2011). The SOC mass in the 1 m of soil in the Sardinilla pasture in 2001 ranged from 10 to 17 kg C m⁻² and in the top 10 cm the average was 3.3 kg C m⁻². Thus, the observed SOC loss of 0.6 kg C m⁻² in the top 10 cm from the conversion from pasture to plantation partially offsets the gain in aboveground biomass (average probably 3 kg C m⁻² in 2011) from the tree cover. This study shows that in an assessment of changes in C stocks from a change in land-use, the soil changes can be significant.

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