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Land cover impacts on aboveground and soil carbon stocks in Malagasy rainforest

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ABSTRACT

Deforestation and forest degradation can impact carbon dynamics and, subsequently, ecosystem functioning and climate change. In this study, we surveyed the influence of such land cover changes on four land cover/uses including closed canopy forest, tree fallow, shrub fallow, and degraded land among 120 study sites. We assessed these changes on total carbon stocks including both aboveground biomass (AGB) and soil organic carbon (SOC) including both topsoil, 0–30 cm, and deep soil, 30–100 cm. The four land cover/uses were located within four regions (Andasibe, Didy, Anjahamana, and Lakato) in the Eastern humid tropical forest of Madagascar. Our results show that total carbon stocks, AGB and soil, average 166 ± 57 Mg C ha^{-1} in which 82% is stored in 0–100 cm of soil surface horizon (55% stored in the topsoil and 27% in deep soil) suggesting the importance of soil pools in the sequestration of atmospheric carbon. The total carbon stocks were significantly higher in closed canopy compared to the other land covers. In lower altitude regions, the total carbon stock was lower ranging from 143.5 Mg C ha^{-1} to 163.7 Mg C ha^{-1}, relative to higher altitude areas where total C stock ranged from 170.6 Mg C ha^{-1} to 186.1 Mg C ha^{-1}. The relative importance of AGB and SOC were reversed in these study sites, with AGB/SOC ratios of 0.37 for Anjahamana, 0.17 for Lakato, 0.21 for Didy, and 0.17 for Andasibe. Climatic factor combined with soil properties could explain the SOC variations across the study regions. High SOC was related to lower precipitation, high clay content and high root development. These results provide an accurate assessment of carbon storage distribution in a tropical region and support the importance of forest conservation and effective land cover management in maintaining carbon storage in ecosystems as tools in climate change mitigation in tropical forests.

1. Introduction

Tropical ecosystems represent a major carbon (C) sink, sequestering large amounts of carbon dioxide (CO_2) from the atmosphere (Ngo et al., 2013). C sequestration and storage also play multifunctional roles in ecosystem services and provide environmental benefits through climate regulation (Brussaard, 2012; Millennium Ecosystem Assessment, 2005). C is initially stored in vegetation including aboveground biomass (AGB) through photosynthesis, and transferred to belowground including root and soil organic carbon pools, and in dead wood and litter pools (Thompson et al., 2012). Tropical forests have a high potential to sequester CO_2, accounting for more than 40% of total C stored in terrestrial biomass worldwide (Day et al., 2013). In fact, Saatchi et al. (2011) estimate that tropical and sub-tropical forests store around 247 Gt C in above and belowground biomass.

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However, these C stocks are affected by natural and human disturbances through land cover changes as a result of deforestation and forest degradation (Day et al., 2013; Guo and Gifford, 2002). Deforestation and forest degradation impact C stock regulation. During forest clearance, C accumulated in AGB is released as CO_2, increasing CO_2 levels in the atmosphere and contributing to global climate change (Day et al., 2013). Furthermore, changes in land cover from forest to non-forest systems result in increased soil loss which could be due to higher rates of flooding and erosion, further enhancing the large fraction of organic matter released as CO_2 (Richey et al., 2002; Thompson et al., 2012).

Studies on the estimation of C stock in tropical areas are scarce in number and the available information on C storage contains large variability, generally associated with the method of C assessment and limited size and number of sampling sites (including replication and sampled area) (Palm et al., 2000; Sierra et al., 2007). Faced with climate change, sustainable management of the terrestrial ecosystem is needed to conserve existing C stocks and enhance these stocks through the sequestration of atmospheric C. Consequently, there is a need to review the effects of land cover change on C storage.

The Intergovernmental Panel on Climate Change (IPCC) reported that deforestation and land cover change, resulting in CO_2 emissions, contribute as much as 24% of the annual CO_2 flux to the atmosphere (IPCC, 2014). Beginning in 2005, with the introduction of Reducing Emissions from Deforestation and Degradation (REDD) as a way for developing countries to reduce emissions, momentum has grown providing innovative ways to reduce greenhouse gas emissions and maintain and enhance C storage in developing countries through forest conservation and sustainable management of various ecosystems, termed REDD+ (Day et al., 2013; Syampungani et al., 2014). REDD+ requires an accurate estimation of C stock in forest and other land cover changes. Estimation of above and belowground C stocks across countries under different land covers accounts for 305 $\mathrm{Mg\,C\,ha^{-1}}$ for primary forest, 218 $\mathrm{Mg\,C\,ha^{-1}}$ for secondary forest, 136 $\mathrm{Mg\,C\,ha^{-1}}$ for tree fallow, 85 $\mathrm{Mg\,C\,ha^{-1}}$ for bush fallow, and 52 $\mathrm{Mg\,C\,ha^{-1}}$ for burned cropland (Woomer et al., 2000).

Natural forest in Madagascar has been severely deforested during the last half century owing to deforestation for timber production and due to land cover practices (Harper et al., 2007; Harvey et al., 2014; Styger et al., 2007). In eastern Madagascar, traditional farming practices of slash and burn, in which the forest is replaced for agriculture by cutting and burning the trees followed by agricultural cycles interspersed with fallow periods, lead to vegetation changes marked by transition of primary forest to grassland (Styger et al., 2007). The first fallow cycle after deforestation is associated with a tree fallow system where vegetation types are dominated by *Trema orientalis* and *Harunganamadagascariensis*. From the second to the fifth fallow cycle after deforestation, endemic shrubs, dominated by *Psidia atlissima* and exotic and invasive species dominated by *Rubus moluccanus* or *Lantana camara*, replace the previous tree fallow species resulting in shrub fallow landscapes. Beyond the sixth fallow cycle herbaceous fallows or grasslands dominate, marked by development of grass species and ferns, *Imperata cylindrica*, and *Aristida* sp. (Styger et al., 2009; Styger et al., 2007). These last systems represent the final stage of ecosystem degradation where lands are abandoned due to low crop productivity.This transition from primary forest to grassland can take between 20–40 years (Styger et al., 2007), and the transitions through these stages area associated with changes in canopy and understory tree density, plant species richness, and C stocks (Devi and Behera, 2003; Harrison, 2011). The influence of these land cover changes in Madagascar on carbon storage in aboveground and soil pools is poorly understood and an accurate quantification of AGB and SOC is required for the assessment of system vulnerability or potential and global C stocks. Increasing interest in measurement of AGB and SOC at 0–30 cm horizon, called topsoil was recently observed in Madagascar forest (Asner et al., 2012; Ramananantoandro et al., 2015; Razakamanarivo et al., 2012; Razakamanarivo et al., 2011; Vieilledent et al., 2012). Assessment of SOC up to 100 cm depth is essential to capture the full soil profile and needs to be examined accurately within different land covers as a large soil C fraction is sequestered in deep soil. Many previous studies have focused on the top soil, less on the deep soil.

This paper aimed to (i) quantify total C stock in aboveground and soil C pools including the top and deep soil C; (ii) determine the effect of traditional Malagasy land cover practices on AGB and SOC; and (iii) identify other environmental factors impacting C stocks.

2. Materials and methods

2.1. Study area

The Ankeniheny-Zahamena Corridor (CAZ) is located in eastern Madagascar. Containing important remnants of Madagascar's humid rainforest, including the majority of the rain forest of low and medium altitude, this area extends over 371,000 ha. The climate of the region is hot and humid tropical with an average annual rainfall of 2500 mm and a mean annual temperature between 18 and 24 °C. The area is characterized by two bioclimate zones, perhumid and humid (Cornet, 1974; Schatz, 2000). Perhumid, the wetter zone, dominates the eastern extent; humid, the drier zone, dominates the west. Soils in CAZ are dominated by ferrallitic soils (Ferralsols according to FAO classification). These high weathered soils are mainly characterized by their red colour due to the presence of iron oxides, the presence of low activity clay (kaolinite), and their low level of organic matter due to their rapid decomposition. In this area, some ferrallitic soils are characterized by a sequence of yellow and red soil horizons. Yellow horizons are often observed in primary and degraded forest. They result from the high weathering and leaching of soil minerals components including clay and iron due to the high precipitation (or rainfall) in the zone (Hervieu, 1967).

Four study regions were selected within the CAZ. The regions were selected to be indicative of CAZ based on a suite of biophysical and environmental variables including elevation, slope, bioclimate zone, climate dynamics, deforestation history etc. The initial selection of regions was further refined through an iterative process to capture (1) a region of rapid recent deforestation and potential impacts on ecosystem services from fallows on relatively un-degraded land (Lakato); (2) a region where reforestation activities have been implemented (Andasibe); (3) a low-lying, accessible, region in the perhumid bioclimate zone (Anjahamana); and (4) a region upstream of the 'rice bowl' of Madagascar. The characteristics of each region are captured in Table 1 and Fig. 1 below. Lakato is located in a high elevation section of CAZ and experiences a humid climate zone. With 1–2 dry season months, the soil in this area is old dominated by association of yellow and red ferrallitic soil. Lakato has a gradient of deforestation chronosequence, including both old as well as rapid recent deforestation, as highlighted above. Andasibe, situated in a high elevation section of CAZ in the south east, is located within the humid climate zone. It experiences 1–2 dry season months, is dominated by yellow or/and red ferrallitic soil, and has old deforestation. Further, reforestation activities have occurred in this region. Anjahamana, situated in a low elevation section of CAZ in the east, has a perhumid climate. This area experiences zero dry season months, and is dominated by an association of yellow and

Table 1
Characterization of sampled regions and the biophysical determinants related to C stocks in different land uses.

							Soil bulk density		Soil texture		Root biomass[b]	
Regions	Land use systems	Obs[a]	Altitude (m)	Slope (%)	MAP (mm)	MAT (°C)	0–30 cm	50–60 cm	0–30 cm Clay (%)	0–100 cm clay (%)	2–10 mm of diameter	<10 mm of diameter
Andasibe	Closed canopy	8	860–1143	16.2–32.6	1746–2198	18.0–19.9	0.7–1.1	1.1–1.5	10.5–32.4	23.7–49.2	37.1(31.0)	77.8(59.7)
Andasibe	Tree fallow	8	824–1096	0.7–37.0	1746–2198	18.0–19.9	0.9–1.2	1.2–1.4	14.6–42.7	14.8–41.4	39.5(15.5)	60.4(19.6)
Andasibe	Shrub fallow	11	795–1003	10.9–30.8	1771–2511	19.0–20.5	0.8–1.1	1.1–1.3	27.4–39.0	17.2–44.0	33.9(18.3)	57.1(26.4)
Andasibe	Degraded land	9	810–1042	1.8–26.5	1771–2163	18.8–19.9	0.8–1.2	0.9–1.4	15.6–44.7	14.1–41.8	31.1(11.8)	51.4(34.7)
Anjahamana	Closed canopy	7	134–559	16.3–27.0	2300–2772	22.0–24.0	0.9–1.1	1.2–1.4	7.5–26.4	18.3–47.5	43.2(9.2)	103.7(21.1
Anjahamana	Tree fallow	7	85–490	14.0–41.0	2344–2732	22.3–23.9	0.8–1.3	1.1–1.7	17.1–28.4	16.1–46.2	38.6(13.6)	67.9(15.5)
Anjahamana	Shrub fallow	7	152–518	9.5–30.0	2344–2713	22.2–23.9	0.9–1.1	1.2–1.4	17.8–35.6	18.4–46.9	28.8(7.9)	56.1(20.2)
Anjahamana	Degraded land	7	148–511	5.5–33.0	2344–2730	22.2–24.0	1.0–1.2	1.2–1.6	15.2–35.8	18.5–44.8	31.4(9.1)	55.8(19.4)
Didy	Closed canopy	7	1014–1200	17.0–29.5	1285–1491	18.5–19.9	0.7–1.0	1.0–1.5	27.9–51.2	20.0–39.5	59.4(14.4)	155.8(54.4)
Didy	Tree fallow	7	952–1101	14.0–29.0	1304–1474	19.0–19.9	0.8–1.1	1.0–1.4	30.6–50.5	23.7–36.2	40.1(9.3)	79.1(17.9)
Didy	Shrub fallow	7	943–1073	9.0–25.0	1287–1474	19.0–19.9	0.8–1.1	1.1–1.4	33.4–49.0	24.8–40.5	40.2(11.8)	73.3(21.4)
Didy	Degraded land	7	930–1089	8.0–28.0	1287–1491	19.0–19.9	0.8–1.2	1.1–1.4	31.8–46.5	25.2–38.6	27.7(16.2)	60.4(31.3)
Lakato	Closed canopy	7	970–1072	20.5–27	1782–1875	18.6–19.0	0.7–0.9	0.9–1.2	13.4–38.5	15.2–34.9	6.2(5.3)	9.9(5.6)
Lakato	Tree fallow	7	978–1035	20.5–28	1794–1906	18.7–19.2	0.7–1.1	0.8–1.2	20.1–36.2	16.0–30.8	1.1(1.0)	2.4(1.9)
Lakato	Shrub fallow	7	905–1047	16.5–27	1768–1900	18.5–19.2	0.6–1.1	0.9–1.2	22.5–35.2	15.7–38.0	1.1(1.8)	1.6(2.5)
Lakato	Degraded land	7	981–1083	19–27.5	1768–1875	18.5–19.0	0.7–1.2	1.0–1.4	9.9–30.3	6.4–35.0	1.8(2.7)	2.9(2.1)

[a] Obs: Number of observation.
[b] Mean value (standard error).

red ferallitic soils; old deforestation dominates in this area. Didy is located in a high elevation area with a humid climate. It experiences 1–2 dry season months per year. This region is also located upstream of a major 'rice bowl' area for Madagascar and, thus, changes in this region may impact this important rice producing region downstream.

2.2. Land cover characterization and the identification of sampling plot locations

Within each region, a very high resolution (VHR) image was then classified into broad land cover/use types to help target the location of sampling plots. The classification scheme was based on Styger et al. (2007) and included closed canopy forest, tree fallow, shrub fallow, and degraded land. Styger et al. (2007) characterized the transition of forest to grassland and, the change in indicator species with repeated fallow cycles along a degradation gradient ultimately with, degraded grassland as an end point as a result of slash and burn agriculture activities. Closed canopy forest provides the undisturbed comparison to the three land uses which correspond to different land degradation gradients. Consequently, these three land use classes help inform the dynamics of carbon storage in the soil and vegetation based on usage current and recent land use patterns. These VHR image classifications were used to help target potential sampling plots within the land cover/use classes within each region. The ultimate location of sampling plots required an iterative process involving repeated field visits to potential plots, expert local input and, ultimately, determined were selected based on accessibility. We sampled at least four replicates of each land cover/use in each study zone (n = 16). In some regions, additional sample sites were identified, resulting in a total of 120 sites for all four regions including: 36 sites in Andasibe, 28 sites in Lakato, and 28 sites respectively in both Anjahamana and Didy. Table 1 summarizes the collected information on the characterization of different land cover/uses in the sampled regions. Based on the field information collected during the surveys, 29 closed canopy forest sites were sampled, 32 tree fallow sites, 29 shrub fallows, and 30 degraded land sites.

2.3. Aboveground C assessment

2.3.1. Data collection

2.3.1.1. Closed canopy. For closed canopy, non-destructive sampling was used to estimate the AGB of forest trees (n = 1935). Within a circular design, with a radius of 20 m, forest inventory parameters were collected including: species name, diameter at breast height (DBH), and total height of each tree (Fig. 2). A hypsometer was used to estimate the total height of the trees.

The Wood Specific Gravity (WSG) of the tree species surveyed was determined based on three approaches: i) WSG values available in international databases (Ramananantoandro et al., 2015; Vieilledent et al., 2012; Zanne et al., 2009); ii) calculations based on the density values (D12%) at 12% moisture that were available from Rakotovao et al. (2012), according to Eq. (1) developed by Reyes et al. (1992); and iii) measurements in the laboratory for the species (30) whose WSG were not available in either databases. For this, 1 cm-long wood core samples from 8 to 13 trees (n = 308) were collected using an electric drill and

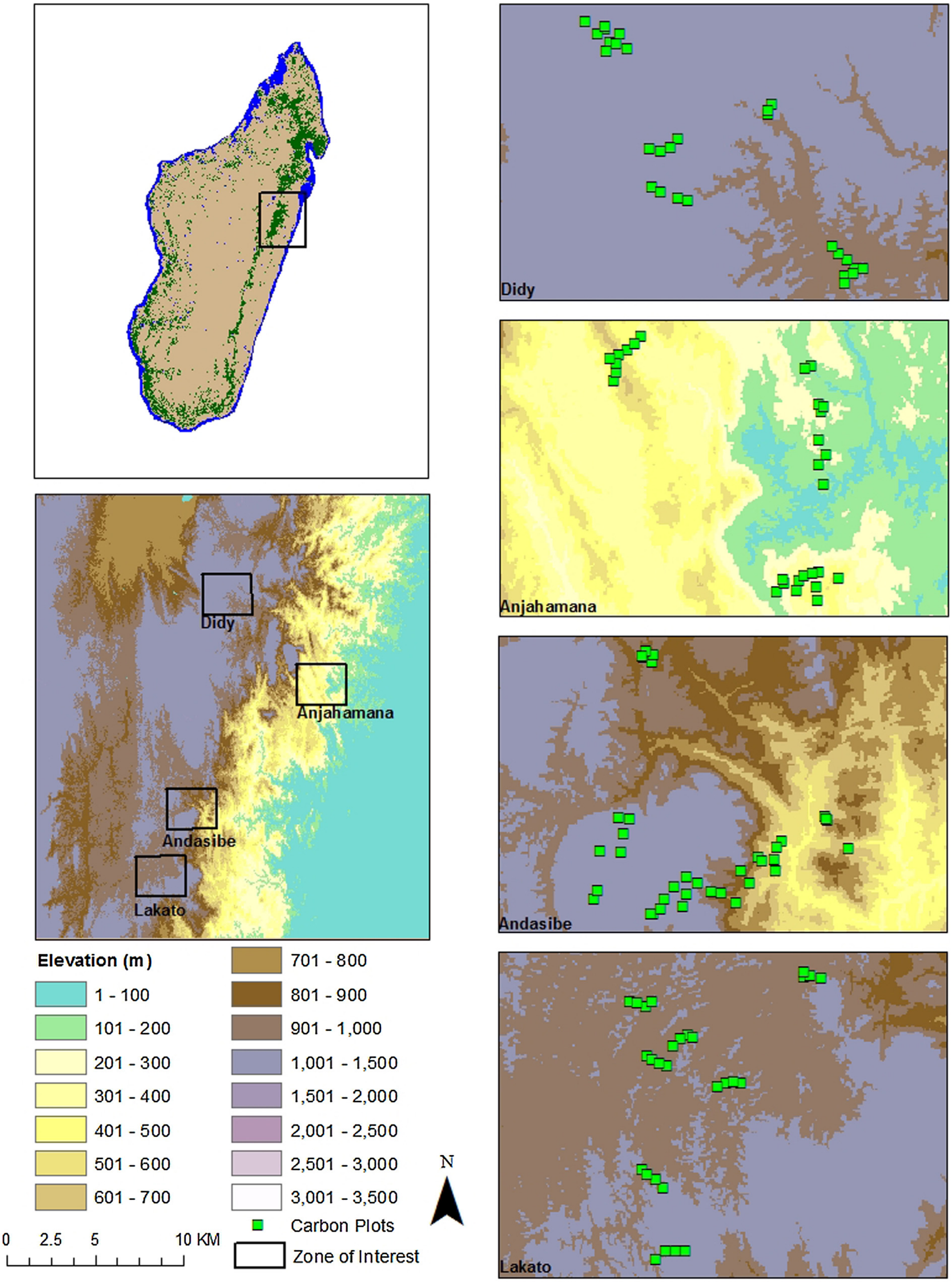

Fig. 1. Location of studied region and land cover surveyed for aboveground and soil C.

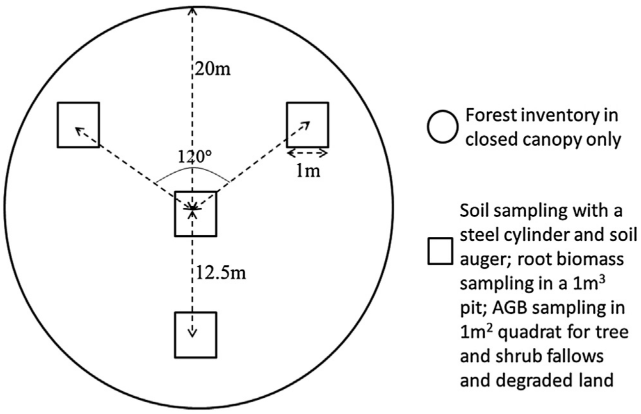

Fig. 2. Sampling design for aboveground and soil data collection in the field.

measured in the laboratory. The cores were water-saturated for 48 h and the saturated volume measured using the Archimedes water displacement method (Wiemann and Williamson, 1988). The cores were then oven-dried (T = 103 °C) and the oven-dry weight recorded. The WSG of a core was defined as its oven-dry weight divided by its saturated volume; WSG of each species was defined as the average WSG of the sampled trees.

$$\mathrm{WSG} = 0.8 \times \mathrm{D}_{12\%} + 0.0134 \quad (1)$$

2.3.1.2. Other land covers. For the three land covers (tree and shrub fallows and degraded land), four subplots were established across each land cover (Fig. 2). Within each subplot, all individual plants were inventoried within a 1 m × 1 m quadrat, cut at ground level and weighed for the AGB assessment.

2.3.2. Carbon calculation

To calculate the C stock of closed canopy forest, AGB was first estimated using the forest allometric equation, Mada I.1 (Eq. (2)) tested for Madagascar. This equation, developed within humid forest sites (with 346 numbers of trees) in the east of Madagascar, is reported to be the best model for humid forests when the three predictive variables: DBH, tree height, and WSG are known as reported by Vieilledent et al. (2012).

$$\mathrm{AGB} = \mathrm{Exp}\,(1948 + (1969 \times \ln(\mathrm{DBH}) + (0{,}66 \times \ln(\mathrm{H})) + (0{,}828 \times \ln(\mathrm{WSG})) \quad (2)$$

Where AGB (kg DW) is dry weight aboveground biomass, DBH (cm) is the diameter of trunk at breast height, H (cm) is the total height of the tree, and WSG (g/cm^3) is wood specific gravity. A C conversion rate of 0.5 was used to calculate the total C content in the dry biomass (Brown, 2002).

For Fallows and degraded land, AGB was quantified after oven-drying and weighing of the collected samples within the 1 m^2 quadrat and extrapolated to a hectare (Condit, 2008). A conversion factor of 0.5 was used to calculate the total C content in the dry biomass.

2.4. Soil carbon assessment

2.4.1. Soil sampling

Soil sampling was performed systematically for both the closed canopy forest and three land uses. Using the soil sampling design illustrated in Fig. 2 soil samples were collected from the four subplots identified in each of the four land covers. Litter horizons were removed during soil sampling. Within each subplot, soil samples were taken with a manual steel auger and steel cylinder (10 cm in height and 8 cm in diameter) at the following depths: 0–10; 10–20; 20–30; 50–60; 80–90 cm for analysis of bulk density and the soil organic C content. Regression analysis was used to generate the entire profile of 0–100 cm.

2.4.2. Soil bulk density

Sampled soils (n = 2400) collected from the cylinder were oven-dried for 24 h at 105 °C, sieved to remove coarse fraction materials (fine roots and gravel or stone) larger than 2 mm in size, and weighed. Soil bulk density was estimated based on the dried weight and volume of the sampled soil.

2.4.3. Soil carbon

To calculate soil C, soil samples (n = 4800) from the steel auger were air-dried, ground finely and sieved through a <0.2 mm mesh to remove fine roots. A principal component analysis was carried out on the MIRS spectral data of all samples in order to select the most representative spectra which will be use for C Walkley and Black (1934) analysis by using WinISI software analysis. In this way, the selected subsample (38.3% of all soil samples) was randomly generated for C Walkley and Black (1934) analysis with wet combustion. The soil C content of the remaining soil was predicted using the Mid-infrared spectroscopy (MIRS) model. For this, all soil samples were analyzed by MIRS (Agilent 4100 ExoScan FTIR (Danburry, Connecticut, USA)) and the spectral data set were used to obtain an accurate model (Fig. 3).

The stock of SOC (Mg C ha^{-1}) was calculated for each soil layer as follows (Eq. (3)) (Parras-Alcántara et al., 2013):

$$\mathrm{SOC} = \sum (\mathrm{BD_i} \times \mathrm{C_i} \times (1 - \mathrm{CF_i}) \times \mathrm{t_i} \times 0.1) \quad (3)$$

Where SOC (Mg C ha^{-1}) is the C stock in soil to 30 and 100 cm depth; BD$_i$ (g/cm^3) is the bulk density of the soil in soil layer i; C$_i$ (g C kg^{-1} of soil) is the soil organic C content in soil layer i; and CF$_i$ (%) is the fractional percentage of coarse fraction >2 mm in the soil profile; t$_i$ (cm) is the thickness of the corresponding layer i (0–10; 10–20; 20–30; 50–60; 80–90 cm). Regression analysis was used to generate the entire profile of 0–100 cm.

The value of SOC from Eq. (3) is calculated based on an equivalent volume of soil because the bulk density of closed

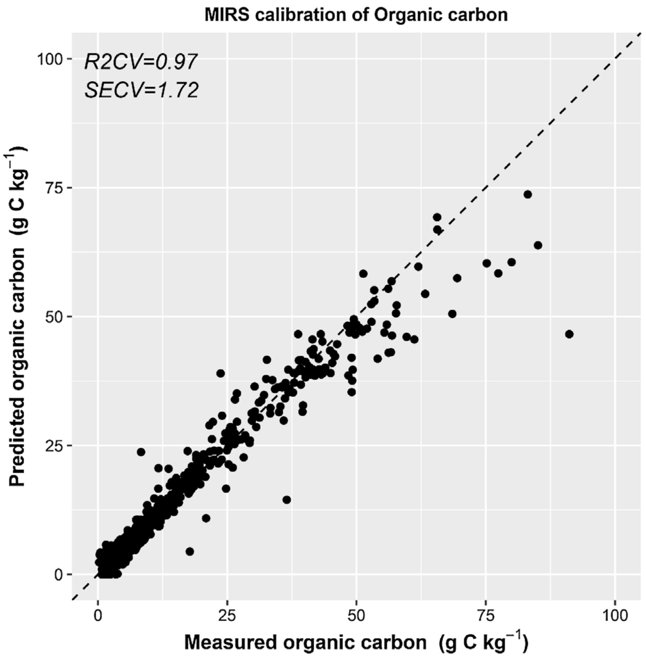

Fig. 3. Prediction model result for SOC based on mid infra-red spectra. R2CV: R-squared of cross validation: SECV: Standard error of cross validation (g C kg^{-1}).

canopy soils is lower than other land covers such as degraded land soils due to the presence of extensive root systems and other gaps; degraded land soils are more compacted. Due of these differences in soil bulk density values, it is more accurate to calculate an SOC assessment based on equivalent soil mass (Ellert and Bettany, 1995) instead of volume references to study SOC changes under different land covers. In this study, SOC at equivalent soil mass was calculated for 0–30 cm and 0–100 cm depth. The equivalent mass for SOC in 0–30 cm horizon was fixed to 3500 Mg C ha^{-1} (Minasny et al., 2013) and 11,500 Mg C ha^{-1} for 0–100 cm SOC. SOC in 30–100 cm depth was calculated from the difference of SOC between 0 and 100 cm and 0–30 cm.

2.5. Soil texture analysis

Soil textural properties were determined in all collected soils (n = 4800). A subset of soil samples (n = 132) was randomly selected for particle size analysis to separate soil fractions. Samples were pretreated with heat and H_2O_2 (35%) to remove organic matter and with NaOH to disperse soil fractions. The soil textural properties of the remaining soil was predicted using the Mid-infrared spectroscopy (MIRS) model from the spectral data set. The following calibration and validation statistics are commonly used to evaluate the accuracy of MIRS model performances: the coefficient of determination (r^2), the standard errors (SE), and the ratio-to-performance deviation (RPD). The results of r^2 in calibration, cross-validation, and prediction were respectively 0.72, 0.74, and 0.95. The values of SE in calibration, cross-validation, and prediction were respectively 7.96 g 100 g^{-1}, 7.56 g 100 g^{-1}, and 3.45 g 100 g^{-1}. The RPD values in cross-validation and prediction were respectively 2 and 4. According to Malley et al. (2004), the MIRS model developed here, based on r^2 and RPD values, can be used as an approximate model for clay content estimation.

2.6. Precipitation and temperature

The mean annual precipitation (MAP) and temperature (MAT) data were calculated from the mean data of 50 years from WorldClim data (Hijmans et al., 2005).

2.7. Statistical analysis

Descriptive statistics including minimum, maximum, mean and coefficient of variation values were calculated for all data to summarize the central trend and to analyze the data variability for each land cover. A boxplot procedure was used to visualize the data and identify the outliers from the datasets. Univariate analyses (ANOVA and Student-Newman-Keuls (SNK) multi-comparison test) were used to test the statistical significance of differences in C stocks in aboveground and top and deep soil between the land covers and study regions. In order to explore the structure of variables with Principal Component Analysis (PCA), correlation matrix between each variable AGB, $SOC_{0\text{-}30}$, $SOC_{30\text{-}100}$, Altitude, Slope, MAT, MAP, $BD_{50\text{-}60}$, $BD_{80\text{-}90}$, $Clay_{0\text{-}30}$, Coarse root (diameter >10 mm), and medium root (2–10 mm diameter) was performed using Pearson correlation. Here, variables with a potential multi-collinearity were excluded. Slope variable was found to have no correlation ($p > 0.05$) with any other variables and it has removed in the list of variables under consideration. The correlation matrix was analyzed by using PCA. Here, most of the selected variables was not normally distributed. Thus, variable standardization was done by scaling to a unit variance before PCA. In order to extract the relevant information from the data table, the structure of the variables and the observations was analyzed using PCA. The resulting PCA components were ranked and the first three components were retained according to the eigenvalue (variability retained for each component) greater than 1 (Abdi and Williams, 2010). All the data table was projected in the first three components, PC1, PC2, and PC3, to generate the loadings (correlation between the component and variable) for all components. In order to facilitate the interpretation, a varimax rotation was applied.

Multivariate regression analysis was used to model SOC from explanatory variables including vegetation cover, altitude, MAP, MAT, Clay content in 0–30 cm and 0–100 cm depth, slope, coarse and medium root biomass. From the initial model (including all the explanatory variables), the collinear predictor variables were selected and removed in the model based on the variance inflation factors (VIFs) calculation. The VIF value lower than 5 for each predictor variables was retained to facilitate the interpretation of the model coefficients. Thereafter, the least significant explanatory variables were selected and removed by step-wise regression analysis where the model was built and improved based on the lowest Akaike information criterion (AIC). The generated model was obtained using lm function in R. All analyses were performed with R software version 3.1.3 (Auguie, 2012; Felipe de Mendiburu, 2012; Kassambara, 2015; R Core Team, 2015; Wickham, 2009; Wickham and Chang, 2015).

3. Results

The aims of this study included: quantifying C stocks in AGB and top and deep soil within different land covers; determining the effect of traditional Malagasy land cover practices; and identifying other biological and environmental variables that impact C stock change.

3.1. Importance of aboveground and soil C pools

The descriptive statistics of C stock for each studied zone are reported in Table 2. In general, the coefficients of variation (CV) for total C stock and 0–100, 0–30, and 30–100 cm SOC (between 24 and

Table 2
Descriptive statistics of carbon stock in different pools in all land uses.

		TotC[a]	AGB[b]	$SOC_{0\text{-}100}$[c]	$SOC_{0\text{-}30}$[d]	$SOC_{30\text{-}100}$[e]
All regions (n = 92)	Average	166.3	30.0	136.2	91.6	44.7
	Maximum	340.8	199.7	250.3	149.1	101.2
	Minimum	24.9	0.6	24.0	20.5	3.6
	CV(%)	34	136	25	24	35
Andasibe (n = 36)	Average	170.6	24.2	146.4	100.3	46.1
	Maximum	285.7	109.0	250.3	149.1	101.2
	Minimum	118.5	3.3	107.7	68.8	21.5
	CV(%)	26	121	21	19	34
Anjahamana (n = 28)	Average	163.7	44.6	119.1	77.0	42.2
	Maximum	336.5	199.7	164.9	102.0	62.9
	Minimum	67.6	7.4	58.6	37.5	21.1
	CV(%)	41	127	18	18	27
Didy (n = 28)	Average	186.1	32.3	153.8	99.3	54.5
	Maximum	340.8	119.8	225.6	141.5	84.1
	Minimum	110.2	2.1	95.9	69.9	26.0
	CV(%)	30	127	19	19	23
Lakato (n = 28)	Average	143.5	20.7	122.8	87.2	35.6
	Maximum	271.7	100.1	210.7	144.6	66.1
	Minimum	24.9	0.62	24.0	20.5	3.6
	CV(%)	40	150	31	29	46

[a] TotC (Mg C ha^{-1}): total carbon stock calculated as the sum of AGB and SOC in 0–100 cm depth.
[b] AGB (Mg C ha^{-1}): aboveground C stock.
[c] $SOC_{0\text{-}100}$ (Mg C ha^{-1}): SOC stock in 0–100 cm depth.
[d] $SOC_{0\text{-}30}$ (Mg C ha^{-1}): SOC stock in 0–30 cm depth.
[e] $SOC_{30\text{-}100}$ (Mg C ha^{-1}): SOC stock between 30 and 100 cm depth).

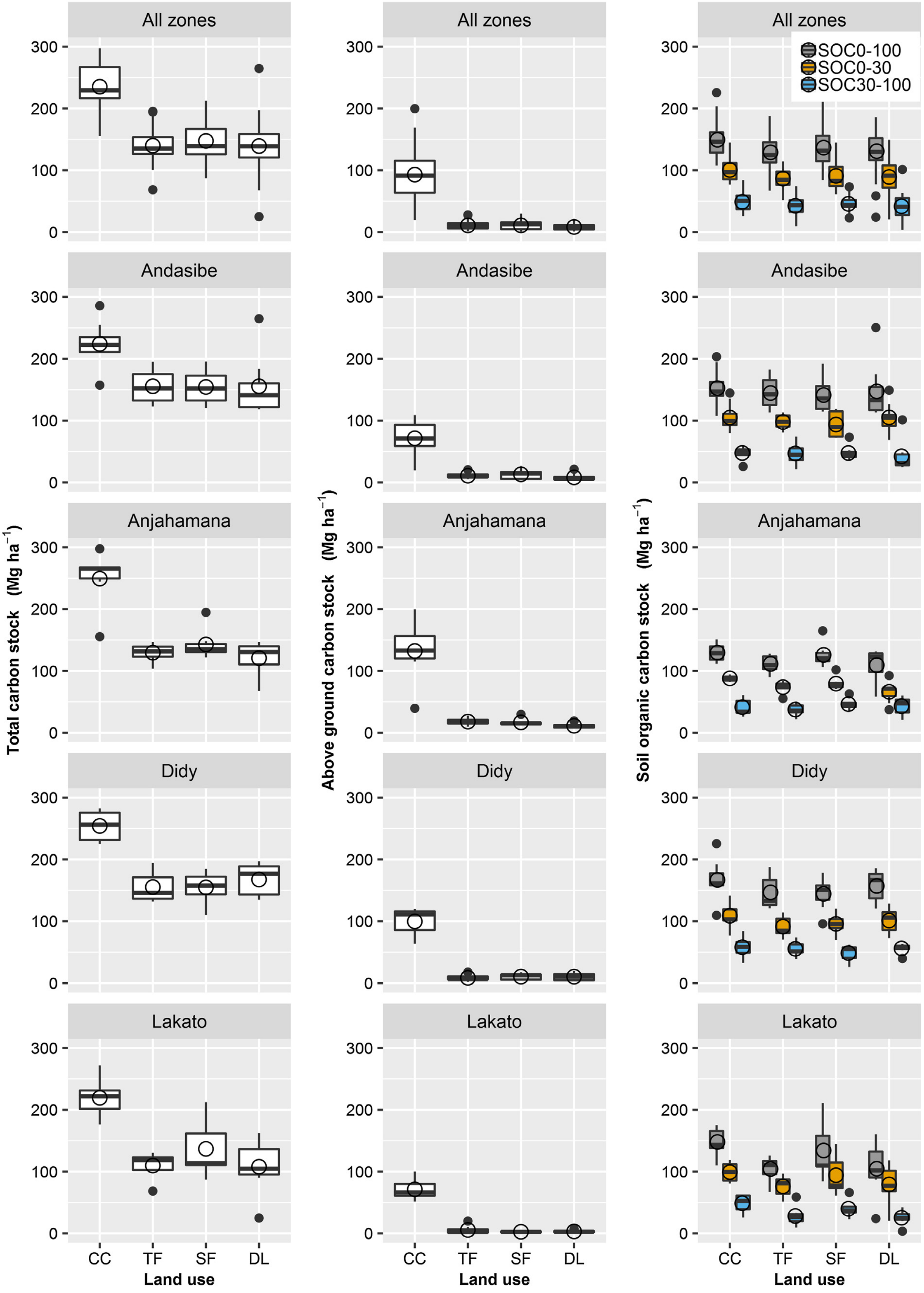

Fig. 4. Total carbon stock, aboveground biomass and top/deep soil organic carbon stock under different land covers in all regions. White circles represent mean values for each land cover. SOC0-100, SOC0-30 and SOC30-100: soil C stock respectively in 0–100, 0–30, and 30–100 cm depth.

35%) were similar, however the CV for the AGB alone exhibited a large variability (between 121%–150%). In general, the contribution of SOC was markedly larger than that for AGB (Fig. 4). In fact, SOC for 0–100 cm depth averaged 82% of total C stock and AGB averaged 18% for all regions. A similar trend was observed for the Didy, Andasibe and Lakato, but not Anjahamana. The AGB:SOC ratios recorded from each zone were 0.21 for Didy, 0.17 for Andasibe, 0.17 for Lakato, and 0.37 for Anjahamana; indicating a higher AGB for Anjahamana compared to the other regions (Table 2). Average total C stocks are larger in Didy (186 Mg C ha^{-1}) compared to those of Andasibe (171 Mg C ha^{-1}) or Anjahamana (164 Mg C ha^{-1}) or Lakato (144 Mg C ha^{-1}).

As illustrated in Fig. 4, our results show that SOC was higher in the topsoil (0–30 cm) than in the deep soil (30–100 cm). Indeed, the topsoil represents 67% of the total SOC (0–100 cm) in contrast with the deep soil, where the proportion of SOC averages 33% of the total SOC (Table 2). The lowest SOC values were recorded from Anjahamana including both the 0–100 cm and 0–30 cm SOC. Average 0–100 cm SOC results were highest in Didy (154 Mg C ha^{-1}) compared to those of Andasibe (146 Mg C ha^{-1}), Lakato (123 Mg C ha^{-1}), and Anjahamana (119 Mg C ha^{-1}). Topsoil consistently stored a larger portion of the total C stock (92 Mg C ha^{-1} representing 55% of the total C stock) than deep soil (45 Mg C ha^{-1} representing 27% of the total C stock).

3.2. Effect of land cover type on C stocks

Considering all of the data from the four land covers, the coefficient of variation for AGB was larger than those for SOC, ranging from 42.5% to 68.6.0% for AGB and 19.7% to 32.1% for the soil pool. Here, AGB at the land cover level is characterized by a low CV value compared with AGB at zone scale. Land cover change had significant effects on total C stock, by impacting the AGB and the top SOC (Table 3 and Fig. 4). Among these significant effects observed in all regions, the AGB and top SOC in closed canopy were markedly higher than other land covers and ranged from 71.4–133.2 Mg C ha^{-1} for AGB and 88.1–108.9 Mg C ha^{-1} for top SOC. The C tree fallow, shrub fallow and degraded land showed relatively similar AGB and SOC stocks, ranging from 8.3 to 10.9 Mg C ha^{-1} for AGB, from 86.4 to 90.9 Mg C ha^{-1} for top SOC (Table 3). In contrast, SOC in 30–100 cm and in 0–100 cm of depth did not significantly change regardless of land cover. A similar trend was observed when the analysis was limited to each zone except that of Lakato.

Furthermore, spatial variation in C stocks was observed among the regions. Specifically, Anjahamana exhibits the most spatial variation among the sites, containing higher AGB for both the closed canopy and tree fallow classes, but lower SOC compared to the others regions (Table 3). In addition, the lowest SOC in Anjahamana was found in degraded land, not exceeding 66 Mg C ha^{-1} in topsoil, and 43 Mg C ha^{-1} in deep soil. Shrub fallow in the four regions contained relatively similar C stocks, except for the AGB. Here the AGB contained 2.6 Mg C ha^{-1} in Lakato compared to 16.8 Mg C ha^{-1} in Anjahamana, 131 Mg C ha^{-1} in Andasibe and 10.5 Mg C ha^{-1} in Didy.

Table 4
Importance of components.

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.7	2.8	1.3	0.9	0.8
Proportion of Variance	34.1%	25.2%	12.0%	8.4%	7.7%
Cumulative Proportion	34.1%	59.3%	71.3%	79.7%	87.4%

Table 3
Mean values of above and below ground carbon stock among the regions.

	C pools[a]		CC	TF	SF	DL
All regions	AGB		92.9 a[b]	10.8 b	10.9 b	8.3 b
	SOC	0–30 cm	100.4 a	86.4 a	90.9 a	89.1 a
		30–70 cm	48.9 a	42.6 a	45.7 a	41.7 a
		0–100 cm	149.4 a	129.0 a	136.6 a	130.8 a
	TotC		242.3 a	139.8 b	147.5 b	139.1 b
Andasibe	AGB		71.5 a B[c]	10.9 b B	13.1 b A	8.2 b AB
	SOC	0–30 cm	104.9 a A	97.8 a A	93.7 a A	105.1 a A
		30–70 cm	47.7 a B	46.9 a AB	47.6 a A	42.2 a AB
		0–100 cm	152.6 a A	144.7 a A	141.3 a A	147.3 a A
	TotC		224.1 a A	155.6 b A	154.5 b A	155.6 b AB
Anjahamana	AGB		133.2 a A	18.1 b A	16.8 b A	11.4 b A
	SOC	0–30 cm	88.1 a A	73.8 bc B	79.6 ab A	66.3 c B
		30–70 cm	41.5 a B	37.6 a BC	46.4 a A	43.1 a AB
		0–100 cm	129.6 a B	111.4 a B	126.0 a A	109.4 a A
	TotC		261.7 a A	129.5 b AB	142.8 b A	120.8 b AB
Didy	AGB		99.7 a AB	8.6 b B	10.5 b A	10.4 b A
	SOC	0–30 cm	108.9 a A	91.4 ab A	95.7 ab A	101.1 b A
		30–70 cm	58.0 a A	55.4 a A	48.6 a A	56.0 a A
		0–100 cm	166.9 a A	146.8 a A	144.3 a A	157.1 a A
	TotC		266.6 a A	155.3 b A	154.8 b A	167.6 b A
Lakato	AGB		71.4 a B	5.6 b B	2.6 b B	3.2 b B
	SOC	0–30 cm	99.2 a A	76.1 b B	94.2 ab A	79.3 b AB
		30–70 cm	48.8 a A	28.1 b C	40.0 a A	25.4 b B
		0–100 cm	148.0 a A	104.2 b B	134.2 a A	104.7 b A
	Tot_C		219.4 a A	109.9 b B	136.8 b A	107.9 b B

[a] AGB (Mg C ha^{-1}): aboveground C stock; TotC (Mg C ha^{-1}): Total C stock calculated as the sum of aboveground biomass C stock and the SOC stock (Mg C ha^{-1}) at 0–100 cm depth.

[b] Different lowercase letters represent significant difference between land cover change at $p < 0.05$.

[c] Different uppercase letters represent significant difference between zone $p < 0.05$.

Table 5
Measure loadings and communalities in unrotated data.

	PC1	PC2	PC3	h^{2*}
AGB	0.15	**0.43**	**−0.71**	0.72
$SOC_{0–30}$	**−0.47**	**0.56**	−0.04	0.54
$SOC_{30–100}$	−0.19	**0.68**	0.13	0.52
Alt	**−0.94**	0.11	0.05	0.89
MAP	**0.88**	−0.28	−0.14	0.86
MAT	**0.91**	0	−0.08	0.84
$Clay_{0–30}$	**−0.56**	0.24	0.24	0.43
$BD_{0–30}$	**0.49**	**0.32**	**0.66**	0.78
$BD_{50–60}$	**0.58**	**0.51**	**0.43**	0.78
Coarse root	0.21	**0.81**	−0.28	0.78
Medium root	0.23	**0.79**	−0.08	0.69
Proportion Variance	0.34	0.25	0.12	
Cumulative Variance	0.34	0.59	0.71	
Proportion Explained	0.48	0.35	0.17	
Cumulative Proportion	0.48	0.83	1	

[*] h^2: communality. Considering the significance of the generated data, minimum loading of 0.32 was chosen accounting for 10% overlapping variance with other items of variables (Tabachnick and Fidell, 2001).

Table 6
Measure loadings after varimax rotation.

	PC1	PC2	PC3	h^{2*}
AGB	−0.18	**0.76**	−0.34	0.72
$SOC_{0–30}$	**0.59**	0.44	0.05	0.54
$SOC_{30–100}$	0.41	0.48	0.35	0.52
Alt	**0.91**	−0.06	−0.24	0.89
MAP	**−0.93**	−0.05	0.07	0.86
MAT	**−0.87**	0.17	0.25	0.84
$Clay_{0–30}$	**0.65**	0	0.1	0.43
$BD_{0–30}$	−0.2	−0.01	**0.86**	0.78
$BD_{50–60}$	−0.28	0.29	**0.79**	0.78
Coarse root	−0.02	**0.86**	0.21	0.78
Medium root	0.00	**0.74**	0.37	0.69
Proportion Variance	0.32	0.22	0.17	
Cumulative Variance	0.32	0.54	0.71	
Proportion Explained	0.45	0.31	0.24	
Cumulative Proportion	0.45	0.76	1	

[*] h^2: communality. Criteria of loadings used for interpretation: greater than 0.50.

3.3. Effect of biophysical determinants on C stocks

Result of PCA including the importance of the variables, the generated variable loadings and communalities were reported in Tables 4–6. The extraction of the first three components covers 71.3% of variance in measure correlation (Table 4). Considering the significance of the generated data in the unrotated data matrix, minimum loading of 0.32 was chosen accounting for 10% overlapping variance with other variables (Tabachnick and Fidell, 2001). “Croassloading” variables (high correlation (>0.32) with two or three components) were found in the unrotated data matrix including SOC 0–30 cm depth, AGB, BD 0–30 cm and 50–60 cm (Table 5). Considering the varimax rotation, these correlations were more precised and more interpretable. In order to improve this observed trend and to facilitate the interpretation of the variable structure, previous study (Costello and Jason, 2005) reported that minimum loading of 0.50 could be selected in case of several crossloaders. This choice largely impacted the correlation of variables with components (Table 6). Here, the first principal component (PC1) explained 32% of the variance in the data which is associated to five variables with the highest loadings. The first component contrasts topsoil SOC, altitude, topsoil clay with climate variables including MAT and MAP. From this, it appears that the high topsoil SOC is associated to high altitude, high clay content in 0–30 cm depth, and low MAP and MAT. The second component (PC2), accounting 22% of the variance in the data, was associated to three highest loading variables. The PC2 is positively linked with AGB, coarse and medium root. The third component, explaining 17% of the variance, is positively associated to bulk density 0–30 and 50–60 cm depth.

The correlation matrix between the AGB, SOC, and their related environmental variables are shown in Table 7. In the ensemble of the data, no significant correlations were observed for AGB and SOC. Among the significant relationships observed, parameters which could affect the C stock pools were altitude, root biomass, soil texture, precipitation and temperature. As observed in the PCA analysis, the AGB was positively correlated with medium ($P < 0.001$) and coarse ($P < 0.001$) root biomasses where the correlation coefficients were similar to those obtained from the total C stock. For SOC in 0–100 cm depth, positive correlations were observed with altitude ($P < 0.001$), clay content in topsoil ($P < 0.001$), and with both medium and coarse root biomasses ($P < 0.01$) and negatively correlated with MAP ($P < 0.001$) and MAT ($P < 0.001$). Similar correlation trends were observed with SOC in top soils. Here, deep SOC in 30–100 cm did not correlated with altitude and MAT. The significant relationship observed between altitude and topsoil C stock, characterized by high clay content in the 0–30 cm layer, is illustrated in Fig. 5. SOC in Anjahamana, located at low altitude, was characterized by a lower clay content in 0–30 cm depth and distinctly separate from the other regions. Didy, located at high elevation, exhibited the highest SOC and high soil clay content.

Results of multivariate regression showed that SOC stocks were closely ($P < 0.001$) related to land cover, altitude, root and clay (Table 8). Considering the strong correlation between altitude, MAT and MAD, the VIFs calculation excluded the climate factors in the model and retained the most influential variable as altitude ($P < 0.001$). Here, land cover change (conversion of forest to fallow and degraded land) significantly influenced SOC in particular at the topsoil and 0–100 cm depth. Influence of land cover change differed according to the considered categories with a higher trend of SOC in closed canopy and shrub fallow. Tree fallow and degraded land are associated with the lowest SOC. Increasing SOC with altitude are mostly related to clay content and root. Thus, altitude (having multicolinearity with temperature and precipitation), texture, and root biomass are considered the main factors controlling SOC change.

4. Discussion

4.1. Carbon distribution between aboveground and soil pools

In this study, all data demonstrate that C stored in the soil pool was higher than the C stored in the aboveground biomass. 82% of total C stock was stored in 0–100 cm of the soil horizon, with more than 55% recorded in the topsoil (0–30 cm). Similar trends were observed by Etchevers et al. (2005) and Lü et al. (2010) in tropical rainforest, secondary forest and agricultural systems. Furthermore, previous authors reported that C of lowland tropical forest is preferentially allocated to aboveground in contrast to montane forests where more C is stored belowground (Girardin et al., 2010; Vieira et al., 2011). This trend is in line with our results where higher SOC was observed in high altitude areas as exhibited by our results at Andasibe and Didy, and higher AGB stock recorded in lower altitude as exhibited by Anjahamana (Table 2). These variations in C partitioning could result from the decreases in AGB occurring at elevations above 1000 m where belowground C tends to increase (Girardin et al., 2010; Leuschner et al., 2007; Moser et al., 2007; Vieira et al., 2011).

Total C stock in closed canopy ranged from 224 to 267 Mg C ha^{-1} according to the zone, and AGB varied between 71 Mg C ha^{-1} and

Table 7
Correlation matrix among the carbon stock pools and their environmental parameters in all regions (N = 92).

Variables	TotC	AGB	SOC_{0-100}[a]	SOC_{0-30}[b]	SOC_{30-100}[c]	Altitude	Slope	MAP	MAT	$Clay_{30}$[d]	$Clay_{100}$[e]	BD_{30}[f]	BD_{50}[g]	C. root[h]	M. root[i]
TotC	–														
AGB	0.82^{***}	–													
SOC_{0-100}	0.71^{***}	0.17	–												
SOC_{0-30}	0.65^{***}	0.15	0.93^{***}	–											
SOC_{30-100}	0.61^{***}	0.16	0.85^{***}	0.59^{***}	–										
Altitude	0.16	−0.07	0.36^{***}	0.44^{***}	0.15	–									
Slope	0.03	0.11	−0.09	−0.15	0.01	−0.11	–								
MAP	−0.18	0.07	-0.39^{***}	-0.40^{***}	-0.28^{**}	-0.89^{***}	0.15	–							
MAT	−0.09	0.11	-0.29^{**}	-0.38^{***}	−0.08	-0.98^{***}	0.09	0.81^{***}	–						
$Clay_{30}$	0.01	-0.20^{*}	0.26^{**}	0.23^{*}	0.24^{**}	0.41^{***}	−0.12	-0.60^{***}	-0.35^{***}	–					
$Clay_{100}$	0.04	−0.01	0.06	−0.02	0.16	-0.26^{**}	−0.10	0.10	0.28^{**}	0.07	–				
BD_{30}	−0.06	−0.08	−0.00	−0.12	0.17	-0.30^{***}	−0.17	0.22^{*}	0.28^{**}	-0.19^{*}	0.14	–			
BD_{50}	0.12	0.10	−0.09	0.02	0.16	-0.41^{***}	−0.07	0.27^{**}	0.42^{***}	−0.15	0.18^{*}	0.70^{***}	–		
C. root	0.52^{***}	0.48^{***}	0.29^{**}	0.23^{*}	0.32^{***}	−0.10	0.04	−0.06	0.21^{*}	0.09	0.12	0.15	0.42^{***}	–	
M. root	0.38^{***}	0.30^{**}	0.29^{**}	0.21^{*}	0.33^{***}	−0.12	−0.11	−0.04	0.20^{*}	0.08	0.07	0.27^{**}	0.43^{***}	0.75^{***}	–

[a] $SOC_{0\text{-}100}$: SOC stock in 0–100 cm depth.
[b] $SOC_{0\text{-}30}$: SOC stock in 0–30 cm depth.
[c] $SOC_{30\text{-}100}$: SOC stock between 30 and 100 cm depth.
[d] $Clay_{30}$: soil clay content in 0–30 cm depth.
[e] $Clay_{100}$: soil clay content in 0–100 cm depth.
[f] BD_{30}: bulk density in 0–30 cm depth.
[g] BD_{50}: bulk density in 50–60 cm depth.
[h] C. root: Coarse root.
[i] M. root: Medium root.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

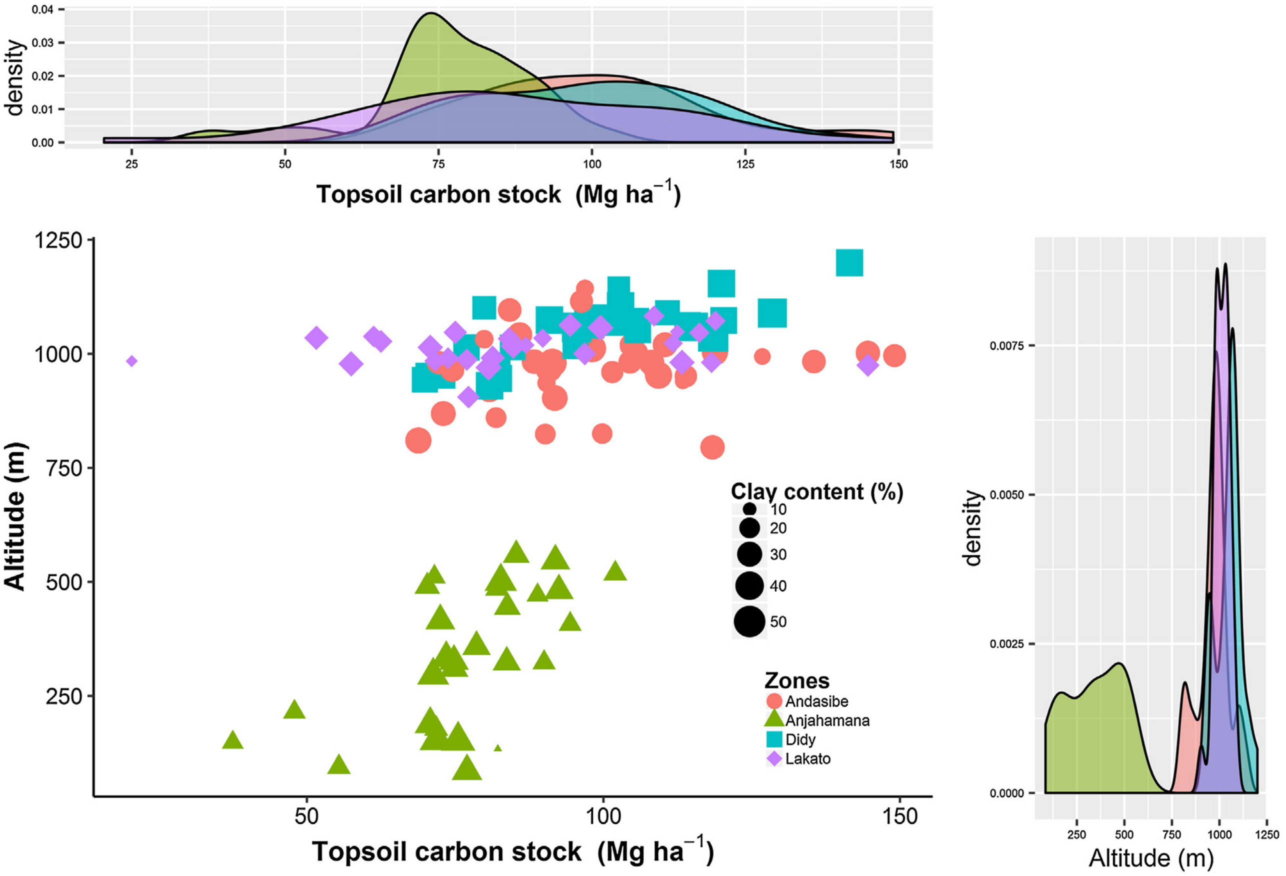

Fig. 5. Relationship between topsoil C stock and their related relevant environment parameters (altitude, topsoil clay content) for each group of zone. Kernel density plot showed the distribution of SOC and Altitude variable values for each zone.

Table 8
Estimates of linear regression model to test the relationship between explanatory variables of soil properties, topography and pedology and SOC. Closed canopy was considered as reference in categorical variables. Significant values of correlation coefficient (differs from 0) was indicated by different signs ($^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

	Coefficient	Standard error	*t* value
SOC 0–100			
Intercept (Closed canopy)	71.167	16.259	4.377***
Categorical variables			
Tree fallow	−15.260	7.487	−2.038*
Shrub fallow	−6.139	7.810	−0.786
Degraded land	−8.757	7.777	−1.126
Continuous variables			
Altitude	0.047	0.009	5.092***
Clay 0–100 cm	0.601	0.338	1.780
Coarse root	0.505	0.133	3.804***
P-value < 0.001			
R^2 = 0.29			
SOC0-30			
Intercept (Closed canopy)	60.898	7.534	8.083***
Categorical variables			
Tree fallow	−8.373	5.013	−1.670
Shrub fallow	−2.900	5.023	−0.557
Degraded land	−4.338	5.217	−0.837
Continuous variables			
Altitude	0.033	0.006	5.708***
Coarse root	0.113	0.041	2.799**
P-value < 0.001			
R^2 = 0.29			
SOC 30–100			
Intercept (Closed canopy)	18.444	8.099	2.277*
Categorical variables			
Tree fallow	−4.480	3.729	−1.201
Shrub fallow	−0.828	3.890	−0.213
Degraded land	−3.007	3.874	−0.776
Continuous variables			
Altitude	0.012	0.005	2.640**
Clay 0–100 cm	0.356	0.168	2.119*
Medium root	0.252	0.066	3.815***
P-value < 0.001			
R^2 = 0.19			

133 Mg C ha^{-1}. These results are in agreement with the previous result reported by Asner et al. (2012) for humid tropical forests of Madagascar where the mean value of C stored in aboveground biomass was 99.5 Mg C ha^{-1}, with a range of 9.3–257.4 Mg C ha^{-1}. These AGB variations could be attributed to several factors including species composition, tree size structure, tree species richness, and abundance of lianas, climate, nutrient conditions, topography, forest age, disturbance, and land management including the past land-use (Foley et al., 2007; Holl and Zahawi, 2014; Lü et al., 2010; Russell et al., 2010). Here, the variation of AGB values may be explained by tree size such as tree heights, 3–26 m for Anjahamana, 5–15 m for Lakato, 4.8–18 m for Andasibe, 4–19 m for Didy, and the proportion of big trees. The proportion of trees with DBH > 40 cm represents 20.3% of all trees with DBH > 20 cm for Anjahamana, 10.6% for Lakato, 7.3% for Didy, and 8.8% for Andasibe.

The SOC values recorded in the 0–100 cm depth of closed canopy (130–167 Mg C ha^{-1}) are similar with the range of SOC estimated for tropical soils (130–160 Mg C ha^{-1}) (Jobbágy and Jackson, 2000), but higher than that found by Lü et al. (2010) in a tropical seasonal rainforest of China (84–102 Mg C ha^{-1}). Our results show that SOC pools in the 0–100 cm depth stored between 49–68% of the total C pool in closed canopy and more than 86% for the other land covers, confirming that less C was stored in the living AGB of a degraded system including the secondary ecosystem such as tree or shrub fallow and the degraded land compared to the natural forest. As a result, C stock in tropical forest is more vulnerable to human activities such as deforestation and traditional slash and burn agriculture than the other land covers (Day et al., 2013).

The 0–30 cm SOC values recorded in this study for closed canopy (between 88 and 109 Mg C ha^{-1}) were higher than the SOC found by Assad et al. (2013) for forests in Brazil (between 27 and 123 Mg C ha^{-1} with mean value of 72 Mg C ha^{-1}) and by Saner et al. (2012) for lowland tropical forests in Borneo (with a mean value of 22 Mg C ha^{-1}). In this study, the higher SOC in the topsoil (0–30 cm) compared to the deep soil (30–100 cm) was similar to the previous results reported by Deng et al. (2014) in China and by Saner et al. (2012) in Borneo. This high potential of topsoil to sequester C is indicative of soil health and soil potential to mitigate climate change (Winowiecki et al., 2015). Here, topsoil has a higher potential to maintain this vital ecosystem service compared to the deep soil. The status of the soil C could affect the biological diversity in soil by maintaining soil fertility through the regulation of C, hydrological, and nutrient cycles and soil structure, thus impacting plant productivity (Brussaard, 2012; Winowiecki et al., 2015).

Fig. 6 summarizes the relationship between 0 and 30 cm SOC and 0–100 cm SOC. As illustrated, the 0–30 cm SOC was well correlated with 0–100 cm SOC ($R^2 = 0.82$; $P < 0.001$). The slope of the regressions of 0–30 cm SOC vs. 0–100 cm SOC for all regions was greater than 1. Again, the correlation held when the analysis was limited to each zone (data not shown). The significant linear relationship between 0 and 30 cm and 0–100 cm SOC suggests the analysis of SOC in the top 0–30 cm could be useful for estimating SOC in 0–100 cm depth. A similar result was found by Deng et al. (2014) where a significant linear relationship was observed between 0 and 100 and 0–20 cm SOC ($R^2 = 0.95$; $P < 0.001$) following cropland conversion. The results from the validation

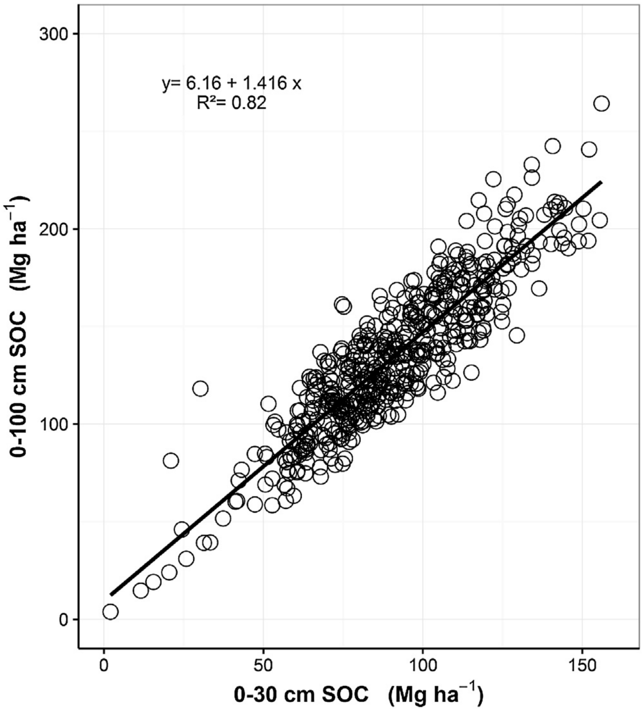

Fig. 6. Relationship between 0 and 30 cm and 0–100 cm soil carbon stock in all regions.

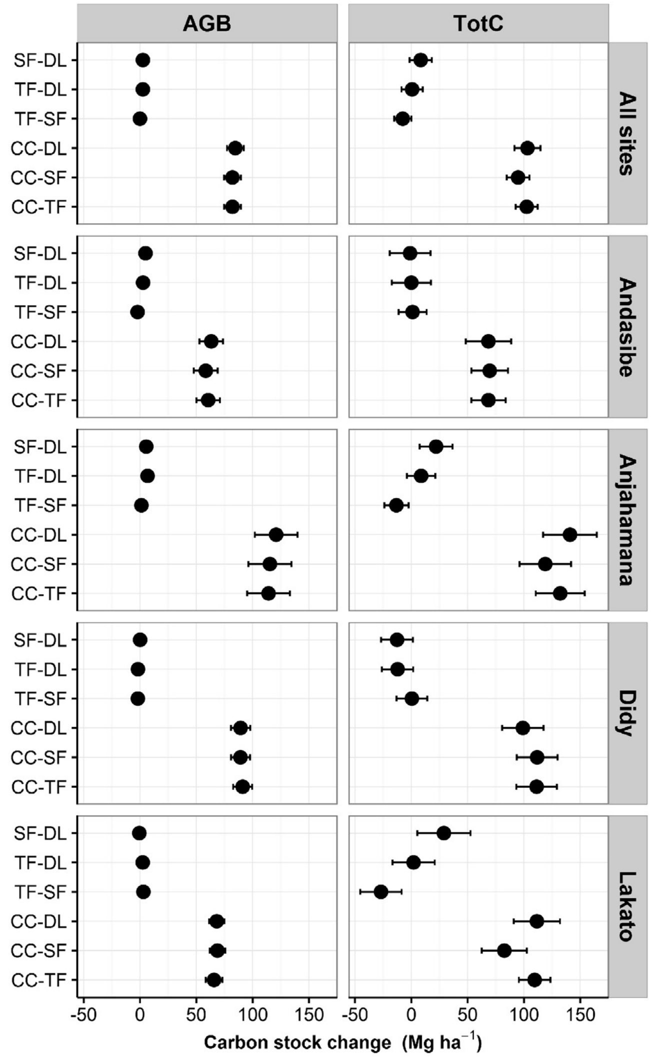

Fig. 7. Influence of land cover change on aboveground and total carbon stock change over the sites (horizontal error bars represent 95% confidence interval).

prediction for 0–100 cm (between predicted and measured 0–100 cm SOC) were relevant in general, with R^2 value of 0.83 (data not shown).

4.2. Changes in C stock under the effect of land covers

If we consider all studied regions, the land cover change from forest to fallow and degraded land led to a significant decrease of total C stock (Figs. 7 and 8). Besides, non-contrasting changes were found between the three land covers: tree fallows, shrub fallows, and degraded land over the sites. These tendency can be explained by the fact that forest vegetation structure and composition was very different compared to those of fallows and degraded land, which seemed to be similar. Effectively, forest land cover is composed essentially of native species dominated by *Eugenia* sp., *Uapacca* sp., *Symphonia* sp. These forest species have lived for several years with a great quantity of understorey vegetation (Styger et al., 2007, 2009). All these biomass affect significantly the total C stocks. However for fallows and degraded land cover, they are largely dominated by shrub species such as *Psidia altissima*, *Lantana camara* and herbaceous as *Clidemia hirta*, *Pteridium aquilinum* and some trees like *Harungana madagascariensis* which produced less biomass than forest and then are very different in term of total C stock in relation to the closed canopy (Styger et al., 2007, 2009). Thus, total C stock values are very closely related with AGB stocks when considering the conversion of forest to other land cover, and related with SOC stocks when considering the conversion of tree fallow to shrub fallow, tree fallow to degraded land or shrub fallow to degraded land. These differences in SOC between land cover considering the age of conversion can be used to explain the trajectory of land cover change.

We compared then SOC changes as degraded land shifts to a forest ecosystem. The land cover change for degraded land to closed canopy resulted in mean SOC accumulation of 14.2% in all regions. The mean values for individual regions were 3.5% for Andasibe, 6.2% for Didy, 18.3% for Anjahamana, and 41.4% for Lakato. Here, the gain in SOC after land cover change of degraded land to forest could be attributed to the long term C sequestration in forest as a result of high C input from aboveground litter and roots, translocation of C from forest floor to mineral soil, and reduced soil C loss from erosion (Chang et al., 2011; Tate et al., 2005). SOC loss occurred following land cover change from degraded land to shrub fallow in Andasibe and Didy respectively by 4.1% and 8.2%. In Anjahamana and Lakato, SOC increased after the land cover change from degraded land to shrub fallow respectively by 15% and 28.2%. In general, the change from degraded land to tree fallow reduced SOC between 0.4–6.6% in all regions. These SOC changes could be explained by organic matter turnover and the age of existing vegetation in the land covers. Effectively, considering the age of fallows, we found that the youngest of these land cover was degraded land while the oldest was the tree fallow. Here, decreasing trend of topsoil SOC was observed from the 5–10 years aged vegetation characterized mainly by land cover change to tree fallow, and these results are in line with the findings of Laganière et al. (2010) who reported a decreasing SOC in younger aged vegetation (5.6% $<$10 years).

So the identified pattern seemed to be that after degraded land, SOC was slightly decreased when the land cover changed to shrub fallow and tree fallow, and increased after conversion of tree fallow to forest.

This trend can be explained by the fact that degraded land is dominated mainly by herbaceous vegetation. The herbaceous plant produces in general a large amount of roots and mainly fine roots which contributes largely to an increase of SOC. This can then explained the high values of SOC stocks in degraded land. The decline of SOC following the conversion of degraded land to fallow (shrub and tree) was probably due to the slight decrease of herbaceous proportion in these land covers with the increase of tree plant. Therefore, the proportion of fine roots declined and even the amounts of residue returned to soil are not enough. For tree development, the mineralization of soil organic matter is accelerated by microbial activity and this can explained the decline of SOC in shrub fallow and tree fallow. Many studies in the literature reported the same trends 0–30 years after cropland conversion to forest where C accumulation is observed in standing biomass rather than in soil in earlier years of ecosystem development (Deng et al., 2014; Laganière et al., 2010). These works reported that the refilling of C by its level of stabilization can occur then later by the increase of SOC.

Here, land cover change differed significantly ($P < 0.001$) with age of fallow decreasing in the order: Degraded land > Shrub fallow > Tree fallow over the regions (Fig. 9). Comparison of topsoil SOC across sites showed that SOC distribution was largely influenced soil properties, climate and topography conditions of the study areas. At the equivalent age of fallow, SOC was significantly different in sites with contrasting conditions, as an example of the higher SOC observed in Andasibe located in higher altitude compared to Anjahamana under tree and shrub fallow. Moreover, Andasibe and Didy have larger topsoil SOC compared to

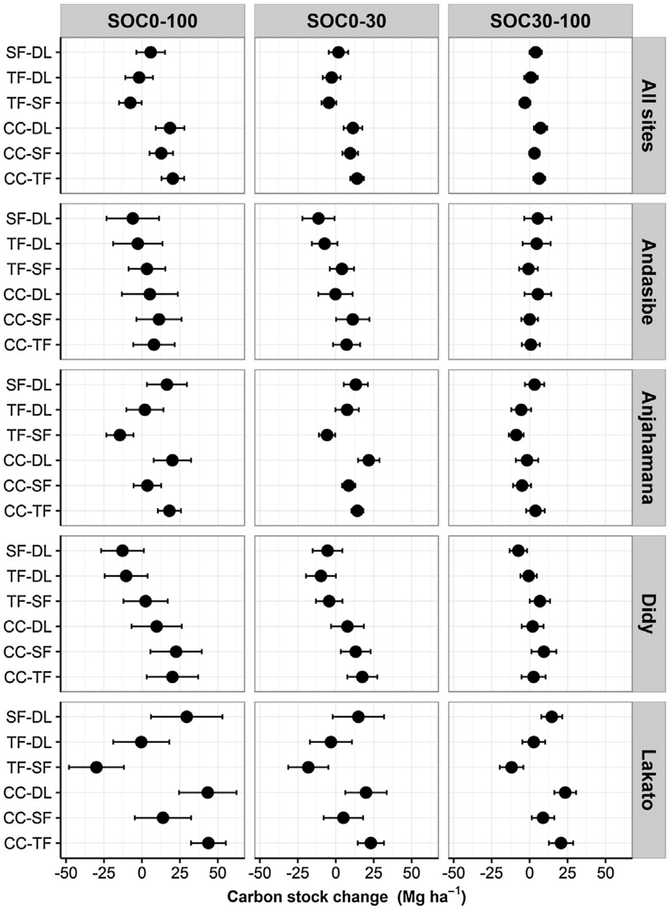

Fig. 8. Influence of land cover change on soil carbon over the sites (horizontal error bars represent 95% confidence interval). SOC0-100, SOC0-30 and SOC30-100: soil C stock respectively in 0–100, 0–30, and 30–100 cm depth.

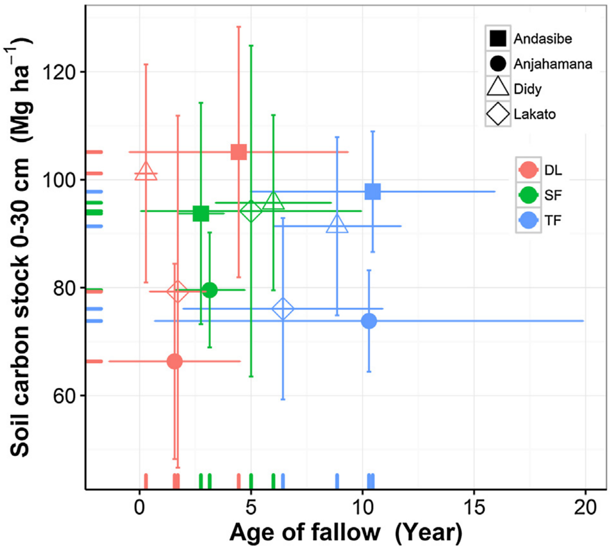

Fig. 9. Relationship between age of fallow and topsoil SOC for each site and land cover.

Anjahamana and Lakato areas in which “tavy” practices (slash and burn system) were very frequent and thus leading to a burning of organic matter.

Different studies reported that climate, elevation, and soil properties exert a large influence on SOC distribution (Willaarts et al., 2015; Parras-Alcántara et al., 2013). Andasibe and Didy located in high altitude presented high soil clay content while Anjahamana and Lakato are characterized by low soil clay content. Anjahamana was specifically located in low altitude with high MAT and MAP. Climate can influence SOC by promoting soil microorganism activity and resulting to the rapid SOC decay under increasing temperature (Knorr et al., 2005).

Furthermore, the decrease in SOC after change of degraded land to shrub or tree fallow systems is related to turnover rates of organic matter into soil where the decomposition of root biomass from herbaceous plants is higher than that of tree roots (Guo and Gifford, 2002). Indeed, the chemical quality of C compounds from tree roots is comparatively different than that from herbaceous roots and it takes more time for tree roots to be recycled and degraded than herbaceous roots (Wellock, 2011). Oyonarte et al. (2008), for example, argue that most of the variability in SOC of natural vegetation in Southern Spain could be related to the land cover history of the different sites. As reported by Adams et al. (1990) and Batjes (2014), factors affecting SOC in the long term include climate, geology, and soil formation, while in the short period, vegetation disturbance and land cover change are identified as the main factors affecting soil C storage

4.3. Factors influencing the C stock

Various environmental factors could also play a key role in the C stock changes of different pools. In this study, changes in C stock were found to be potentially related to altitude, precipitation, temperature, soil texture, and root biomass. Bird et al. (2001) reported the same observation; SOC was controlled by factors including climate, soil texture, land cover, and topography.

Considering the multivariate regression analysis, we found significant changes in SOC among altitude ranges ($P < 0.001$). This can be attributed to biological processes controlling the organic matter turnover along the altitude. Sousa Neto et al. (2011) observed that soil temperature decreases with altitude, this is in agreement with our results. The increase of temperature at lower altitudes could intensify the soil microbial respiration and the decomposition rate of plant residues, leading to SOC losses and, consequently, low amounts of SOC (Biasi et al., 2008; Dorrepaal et al., 2009; Vieira et al., 2011). Our results support this, the lowest SOC results in the first meter were found in the lowest altitude area of Anjahamana, in contrast with the high SOC recorded in the high altitude zone of Didy and Andasibe. A combination of high precipitation and high temperature has also been found to negatively influence SOC, probably due to SOC mineralization stimulation (Fantappiè et al., 2011). Our results reflect this, the higher precipitation and temperature regions including Anjahamana and Lakato present low SOC compared to Didy and Andasibe.

Our results show that the SOC were significantly positively correlated with the clay content in topsoil. This is in line with results reported by Jobbágy and Jackson (2000) and Parras-Alcántara et al. (2013), they found significant correlation between soil texture and SOC. Indeed, SOC is highly associated with clay particles and non-crystalline minerals which provide organic matter protection and stabilization (Jobbágy and Jackson, 2000). Here, our results demonstrate that the high C stock in soil pools were related to the high clay content in topsoil found in Didy and Andasibe regions (average value of 39.6% and 29.57% respectively), in contrast to the low C stock observed in the low clay content areas of Anjahamana (average value of 22.7%) and Lakato (average value of 27.2%). Any significant relationship observed between SOC and AGB, suggests the large influence of clay content status on SOC as reported by Mekuria and Aynekulu (2013) and Willaarts et al. (2015).

Root biomass was also positively correlated with AGB ($P < 0.001$) and with SOC ($P < 0.01$). We found significant change ($P < 0.001$) in root biomass in land covers marked by higher values of coarse and medium root biomass present under closed canopy compared to the other land covers. Our AGB and SOC showed a similar trend for closed canopy and the other land cover. This increase in SOC under closed canopy may be explained by root turnover and quality of C inputs (Jobbágy and Jackson, 2000; Ngo et al., 2013). Indeed, SOC are largely affected by vegetation types generating litterfall input through decay. The high lignin and soil carbon:nitrogen (C/N) ratios found in forest indicate the low decomposition of organic matter and, consequently, C accumulation in surface soils compared to the other land covers (Austin and Vitousek, 1998; Jobbágy and Jackson, 2000). High root biomass is also reported to generate higher aboveground biomass in montane forest and increase productivity leading to increased C stock which could explain the higher relationship of AGB and root biomass (Sierra et al., 2007).

5. Conclusions

Our results highlight the high variability in total C stocks (AGB and SOC) that exists across the studied land covers and regions. However, the average C stocks recorded in soil pools were significantly higher, by 82%, than those in aboveground biomass pools; 55% of total C stock was stored in the topsoil horizon and 27% in the deep soil. In general, closed canopy had higher total AGB and topsoil C stocks compared to the other land covers. This can be explained by vegetation type, structure, and historical land management. Other environmental factors were found to influence C stock in different pools including altitude, climate, soil texture and root biomass. While this research generated improved estimates of C storage and preferential allocation in different land covers, and the impact of environmental variables, further investigation into additional C pools including dead wood, litter and belowground C pools is needed to further understand ecosystem functioning.

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